











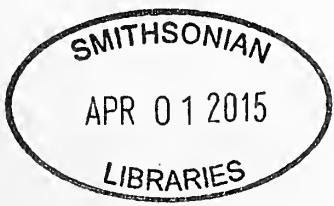


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to malacology.*



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# THE NAUTILUS

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# New viviparid gastropods from the end Cretaceous and early Paleogene of the Williston Basin, USA and Canada

**Joseph H. Hartman**

University of North Dakota  
Harold Hamm School of Geology and Geological Engineering  
81 Cornell Street Stop 8358  
Grand Forks, ND 58202 USA  
joseph.hartman@engr.und.edu

## ABSTRACT

Three new species of Viviparidae (Caenogastropoda) are described and illustrated from the Williston Basin of North Dakota, Montana, and Saskatchewan. The new *Campeloma*, with strong shoulder development, is separated from others in geologic time by recognizing its distinctive morphological features. *Campeloma acroterion* new species occurs primarily in Lancian North American Land-Mammal Age (NALMA) strata, survives the Cretaceous–Paleogene extinction event, and ranges into the late Puercan NALMA (end Cretaceous to lower Paleocene; Hell Creek Formation into Tullock Member of Fort Union Formation and equivalents). *Campeloma nebrascense whitei*, a larger and more rounded, but shouldered species, appears as a derivative species in younger rocks, followed and partially coeval with *C. n. nebrascense*, which is without shouldering. *Viviparus purgatorius* new species and *V. codomorphus* new species are species of discovery. Neither species are common and the few specimens collected have been assigned to more common taxa. *Viviparus purgatorius* ranges from the Puercan to Torrejonian (lower and middle Paleocene; Tullock Member and Ravenscrag Formation), and *V. codomorphus* may be only known from the Torrejonian NALMA (middle Paleocene; upper part of the Ludlow Member of the Fort Union). These species of *Viviparus* appear derived from more sculptured forms of *V. thompsoni* also present in Laneian strata of the Lance and Hell Creek Formations. With the regression of the Cannonball Sea and the expansion of Laramidia in the early late Paleocene, viviparids radiate, becoming far more numerous, diverse, and morphologically variable until the end of the Laramide Orogeny (~mid Eocene) with North America as one continental landmass.

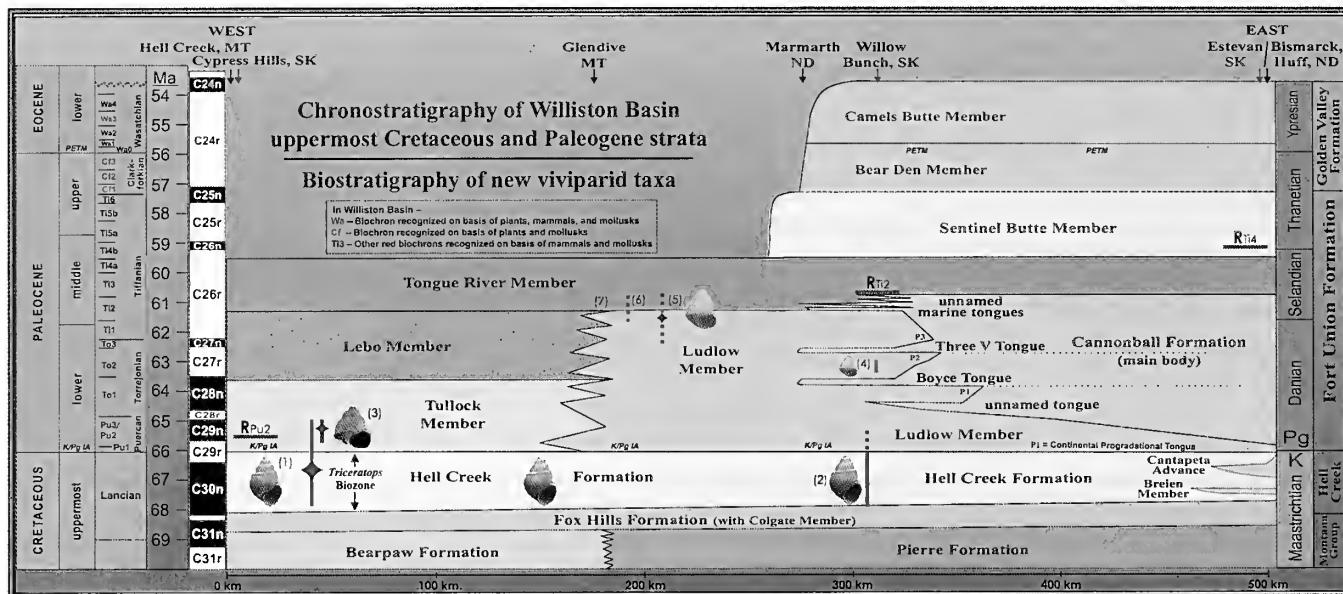
## INTRODUCTION

This paper introduces new viviparid species that have been recognized by the author for some time (Hartman, 1984). Publication of a monograph on fossil Viviparidae is under construction, but still too far off to delay naming of a number of taxa. The continental molluscan record of the Cretaceous and Paleocene of Laramidia is more diverse than typically known. Three new viviparid species

add to the known species richness during intervals of geologic time that are, in part, less populated by gastropods. These species are also in chronostratigraphic succession in the Williston Basin of North Dakota, Montana, and Saskatchewan. They include *Campeloma acroterion* (Lancian into Puercan NALMA), *Viviparus purgatorius* (Puercan into Torrejonian NALMA), and *Viviparus codomorphus* (Torrejonian into Tiffanian NALMA), ranging from latest Cretaceous to early late Paleocene (Maastrichtian to Selandian). These species occur in the Hell Creek Formation, and Tullock, Ludlow, and Tongue River Members of the Fort Union Formation in the United States, and the Ravenscrag Formation in Canada (Figure 1).

## MATERIALS AND METHODS

The taxa introduced are based on examination of fossils from more than 1100 continental molluscan localities (see Appendix 1; e.g., Hartman, 1984, Appendix 3, locality register; Hartman, 1998, fossil localities; Hartman and Roth, 1998, Appendix, Bighorn Basin locality register). This effort originally comprised the dissertation studies of the author (Hartman, 1984), but now includes many years of subsequent field and museum studies (e.g., Hartman, 1989, 2004; Hartman and Kihm, 1992; Hartman and Roth, 1998; Hunter et al., 1997; Hartman and Kirtland, 2002; Scholz and Hartman, 2007; Hartman et al., 2014). Many of the specimens examined were collected by others (e.g., Saskatchewan record) and are deposited at institutions (see list under Abbreviations) visited by the author. Important primary documentation was available for many localities at institutional archives. When possible, specimens were borrowed for additional study to compare with in-house specimens. In addition, several thousand photographs were taken of museum specimens to augment the borrowed material, and for use in measuring specimens. Only a few measurements of Cretaceous or Paleogene continental mollusks were available from the literature. Most of these measurements are in reference to types, and do not provide a



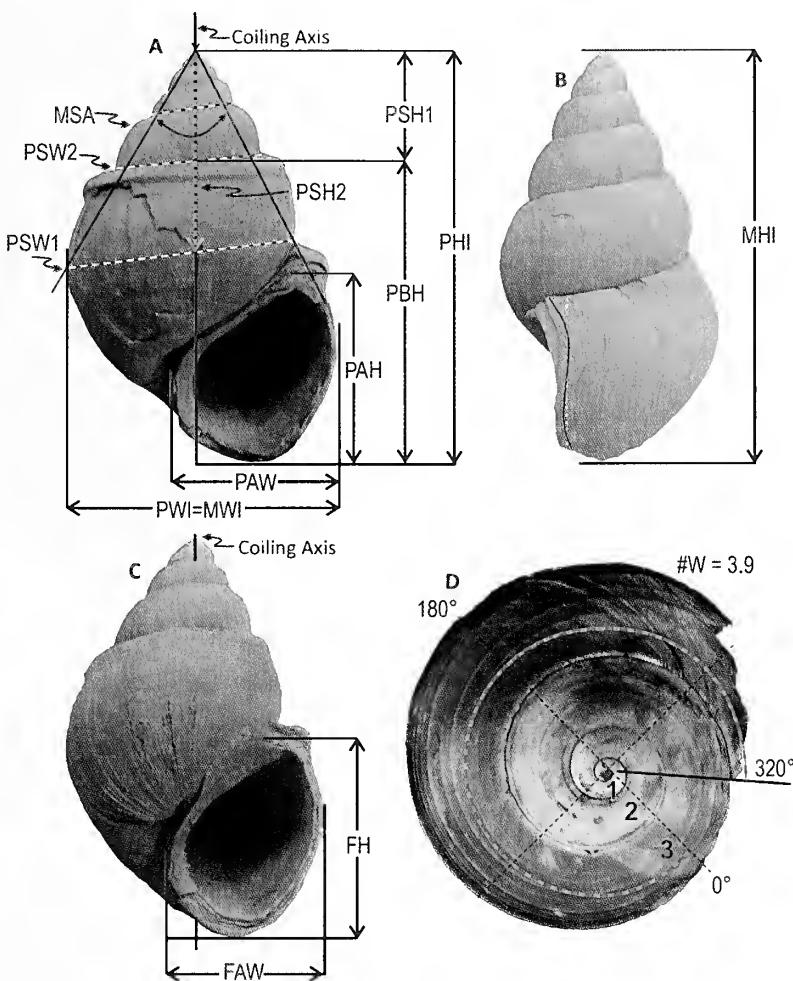
**Figure 1.** Chronostratigraphic placement of new viviparid species in a chronostratigraphic correlation of Williston Basin uppermost Cretaceous and lower Paleogene strata. Chart based on Lund et al. (2002), Hartman et al. (2005) and is revised using geochronologic and other data from Murphy et al. (2002), Clechenko et al. (2007), Secord (2008), LeCain et al. (2014), Ogg et al. (2014), Vandenbergh et al. (2014).

basis for a quantitative analysis of shell form, plus the methods by which the measurements were taken are virtually always unknown (e.g., specimen orientation; see measurement methods below). One of the purposes in redescribing previously named taxa (Hartman, 1984) was to provide a more rigorous quantitative database upon which to compare fossil viviparid morphologies. The quantitative measurement parameters used here to describe the introduced species (summarized in later tables) are used in diagnoses, descriptions, tables, and graphs in the systematic part of this report (and Hartman, 1984). Measurement types (and their abbreviations) are given in Table 1. Measurement parameters are illustrated in Figure 2. Individual shell measurements are given in Appendix 2.

**Abbreviations and Notes:** W = number of whorls; SD = standard deviation; min. = minimum; max. = maximum; n = number of specimens; loc. = number of localities. K/Pg = Cretaceous–Paleogene, La = Lancian, Pu = Puercan, To = Torrejonian, Ti = Tiffanian, Cf = Clarkforkian, Wa = Wasatchian, NALMA = North American Land-Mammal “Ages.” HC = Hell Creek, LA = Lance, LU = Ludlow, TU = Tullock, LE = Lebo, TR = Tongue River, FU = Fort Union, RA = Ravencrag. AMNH-FI = American Museum of Natural History, Fossil Invertebrates, New York; GSC = Geological Survey of Canada, Ottawa; MCZ = Museum of Comparative Zoology (Harvard University), Cambridge; UND-PC = University of North Dakota, Paleontological Collection, Grand Forks; UND-JHH = Hartman collection at UND; UCMP = University of California Museum of Paleontology, Berkeley; UMPC = University of Minnesota, Paleontological Collection, Minneapolis; USNM-PAL = U.S.

**Table 1.** Measurement Abbreviations.

Measure	Description/How Measured (see Fig. 2)
#W	Number of whorls or revolutions; counted on complete specimen
#W-MHI	Number of whorls; counted on maximum height of a slightly incomplete specimen
#W-MS	Number of whorls; counted on an incomplete specimen (MS = maximum seen)
MSA	Mean spire angle
MHI	Maximum shell height; measured with hand calipers or right lateral view
PWI(MWI)	Width measured from photograph; measured with calipers
PHI	Height; measured from photograph
PSH1	Spire height; measured from photograph
PSH2(MSH)	Spire height 2 = mean spire height; measured from photograph
PBH	Body height = last-whorl height; measured from photograph
PSW1(MSW)	Spire width 1 = mean spire width; measured from photograph
PSW2	Spire width 2; measured from photograph
PAW	Aperture width; measured from photograph in plane of axis of coiling
PAH	Aperture height; measured from photograph in plane of axis coiling
FAW	Flush aperture width; measured from photograph in plane of aperture
FAH	Flush aperture height; measured from photograph in plane of aperture
GLA	Growth-line angle; measured in right lateral view from photograph
MSW/MSH	Ratio approximates mean spire angle
MSW/PSW2	Ratio = last-whorl expansion ratio



**Figure 2.** Gastropod Measurement Abbreviations. Figures 2A–D represent three standard photographic views from which specimen measurements were acquired (see Table 1 for abbreviations). **2A.** Apertural. **2B.** Right lateral, growth-line angle (GLA) is vertical (one-dashed line) in species of *Campeloma*. **2C.** Apertural flush. **2D.** Apical, number of whorls (revolutions) counted with use of a protractor. **2A** and **2C.** *Campeloma acroterion*. **2B.** *C. nebrascense nebrascense*. **2D.** *Viviparus purgatorius*.

National Museum of Natural History, Invertebrate Paleontology Collection, Washington, D.C. See also abbreviations in Appendix 1 (Locality Register).

All United States quadrangles are USGS 7.5-minute, 1:24,000, topographic maps, NAD27CONUS datum, with 20 ft (6.1 m) contour intervals. All Canadian maps are Natural Resources Canada (was Department of Energy, Mines and Resources), 15×30 minute, 1:50,000, topographic maps, NAD27 datum, with 25 ft (7.6 m) contour intervals.

Two Appendices with supplementary data to this work are posted online at <http://nautilus.shellmuseum.org>. **Appendix 1** is a Locality Register describing in detail the localities discussed herein. **Appendix 2** consists of three tables with measurements of all specimens of the three species presented in this study.

#### Explanation of Figure 1

The correlation of strata presented in Figure 1 uses a Hell Creek Formation duration of 1.8 million years

(Wilson, 2005). Although no single value can be correct, the Fox Hills Formation in the western part of the Williston Basin is approximated as the top of the *Jeletzkytes nebrascensis* ammonoid zone (Landman et al., 2007; Vandenbergh et al., 2014). PETM (= Paleocene-Eocene Thermal Maximum) and the K/Pg IA (= Cretaceous-Paleogene Iridium Anomaly, or similar evidence, e.g., fern spike) are located approximately along a transect from Bismarck to Marmarth (see Hartman et al., 2002, for citations; Clechenko et al., 2007; Hartman et al., 2014). The approximate locations and biohorizons of type localities in Figure 1 are indicated by “?” on vertical local biostratigraphic range lines. RPu2 (= Ravenscrag Formation, Puercan 2, etc.) symbols are overlays of the approximate NALMA known or interpreted from the Ravenscrag Formation in the Cypress Hills of southernmost Saskatchewan (see text). Figure 1 notes include: 1) *Campeloma acroterion* is described from the uppermost Cretaceous Hell Creek Formation in its type area of Hell Creek (Table 3), north of Jordan, Montana. *C. acroterion* is also known from the lowermost Paleocene

Tullock Member (Fort Union Formation) in the western part of the Williston Basin. 2) *C. acroterion* is not well known from the lowermost Paleocene of easternmost Montana or North Dakota. *C. acroterion* is known from a number of other uppermost Cretaceous formations in the USA and Canada. 3) *Viviparus purgatorius* is described from the lowermost Paleocene Tullock Member in McCone County, Montana (see Table 7). *V. purgatorius* is also known from the Bear Member (Fort Union Formation) in the Crazy Mountains Basin, Montana, and from the lower part of the Ravenscrag Formation in Saskatchewan. 4) *V. codomorphus* is described from the Ludlow Member (Fort Union Formation) between the tongues of the Boyce and Three V Tongues of the Cannonball Formation in the Little Missouri River valley, Slope County, North Dakota. 5) The type locality of *V. codomorphus* is from the east flank of the Cedar Creek Anticline in what the author interprets as uppermost part of the Ludlow Member in easternmost Montana. 6) *V. codomorphus* also occur at an ill-defined location in the vicinity of Wibaux, Wibaux County, Montana. This occurrence might place it in the Tongue River Member. 7) The Ekalaka Member (Fort Union Formation) does not occur between the Ludlow and Tongue River Members (Fort Union Formation) along the traverse of this profile (see Vuke et al., 2007).

## STRATIGRAPHY

The litho- and chronostratigraphy of the Cretaceous-Paleogene boundary-interval strata in the northern Great Plains and intermontane basins of the United States and Canada are subjects of continual refinement (see citations above and Figure 1). Field notes and other unpublished information were used to augment collection and/or published accounts of species records to better geographically plot and place specimens in relative stratigraphic position. All type localities were examined by the author, with the help of others, on more than one occasion. Stratigraphic and sedimentologic data were collected along with other elements of the local fauna. The three taxa described are presented in stratigraphic succession. *Campeloma acroterion* is known primarily from the uppermost Cretaceous Hell Creek and Lance Formations and also from formational equivalents. It also is one of the few species in the northern Great Plains known to cross the K/Pg boundary, with occurrences in the Tullock Member of the Fort Union Formation. *Viviparus purgatorius* is primarily known from localities in the Tullock Member and is well documented from the lower and middle part of the Ravenscrag Formation in Saskatchewan. The stratigraphic horizon of the type series of *V. codomorphus* is the least well documented, in occurring at the top of a large, grass-covered hill on the flank of an anticline. Vuke et al. (2003) mapped this silcrete-bearing section as Tongue River Member, but previously mapped the area as equivalent to the upper Ludlow Member (Vuke

et al., 1986). The author is inclined to map it as Ludlow Member (see later discussion below and with Figure 1). In North Dakota, *V. codomorphus* occurs between the Boyce and Three V Tongues of the Cannonball Formation in the upper part of the Ludlow Member (above the T Cross lignite of Moore, and below the silcrete horizon at the top of the member [Hartman, 1993]).

A NALMA can be interpreted for each species. The holotype of *Campeloma acroterion* is Lancian and ranges to Puercan 2-3 (Figure 1, note 1). The species duration is estimated to be about 3 million years. The holotype of *Viviparus purgatorius* is Puercan 2-3 and likely ranges to mid Torrejonian (Figure 1, note 3). The duration of the species is also estimated to be about 3 million years. The holotype of *V. codomorphus*, if the specimens are from lowermost part of the Tongue River Member, is lower Tiffanian (see Figure 1, notes 4, 5, 6). The holotype may be approximately equivalent in age to the Ollie North local fauna, which has yet to receive study to assign a NALMA. Lithomarker correlation studies by the author place the Ollie North about 20 m below the silcrete-White-Marker-Bed used to demarcate the top of the Ludlow Member (Belt et al., 1984). The duration of the record of *V. codomorphus* on the basis of mammals is estimated at about 2.5 to 3.0 million years (depending on lithostratigraphic interpretation).

## SYSTEMATICS

Class Gastropoda Cuvier, 1797

Subclass Orthogastropoda Ponder and Lindberg, 1996

Superorder Caenogastropoda Cox, 1960

Order Architaenioglossa Haller, 1892 [paraphyletic]

Superfamily Viviparoidea Gray, 1847 \*

\*Suprafamilial classification after de Bruyne (2003) and Bouchet and Rocroi (2005) after The Taxonomicon compilation (see sources therein).

Family Viviparidae Gray, 1847

Subfamily Lioplacinae Gill, 1863

### ***Campeloma Rafinesque, 1819***

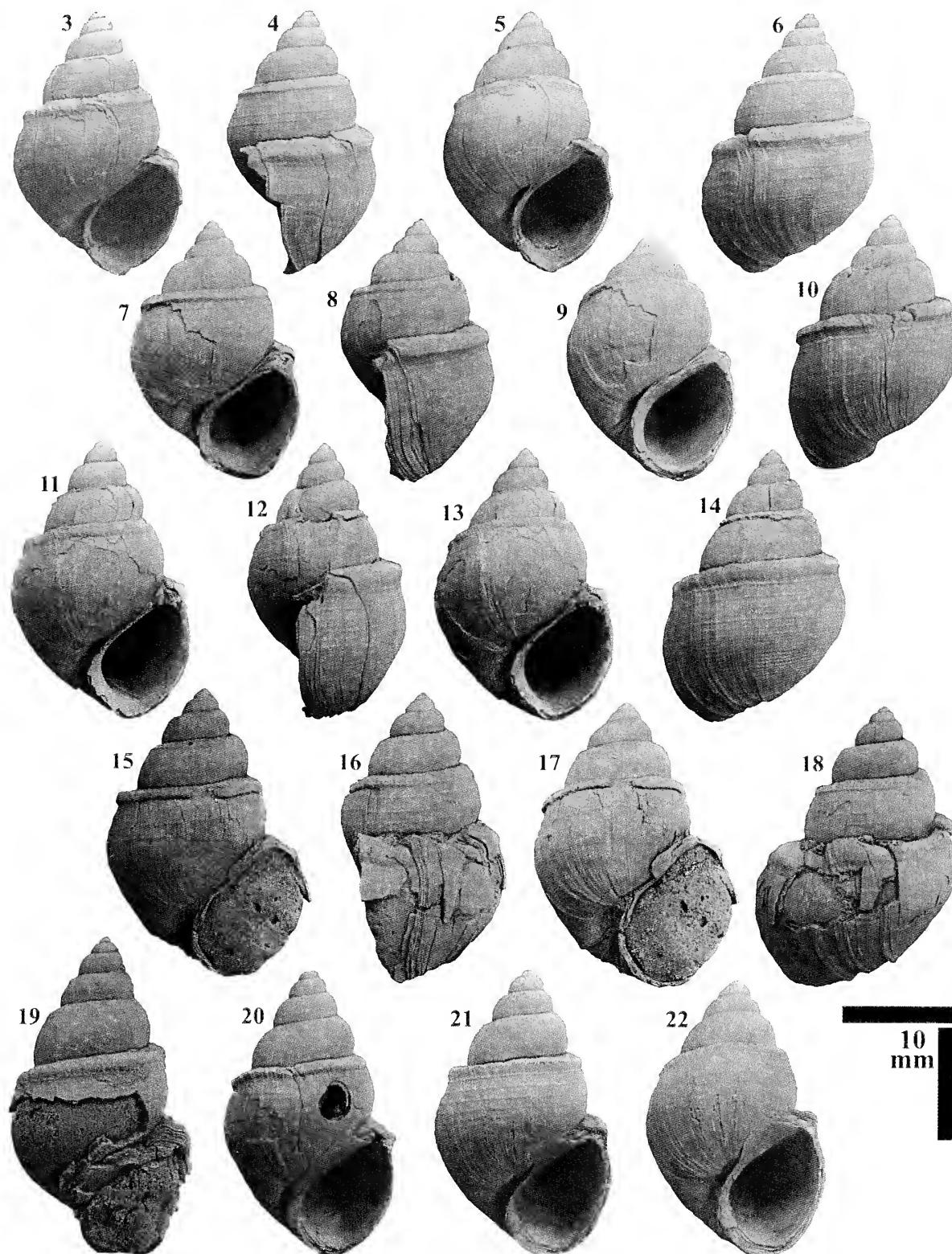
**Etymology:** *campeloma* (Greek), a bending, and (Greek) a margin, “in exact keeping with the sigmoid character of the aperture of all the species of the genus” (Call, 1883, p. 605).

**Type Species:** *Campeloma crassula* Rafinesque, 1819 (available; see, ICBN, 1999, Opinion 1931).

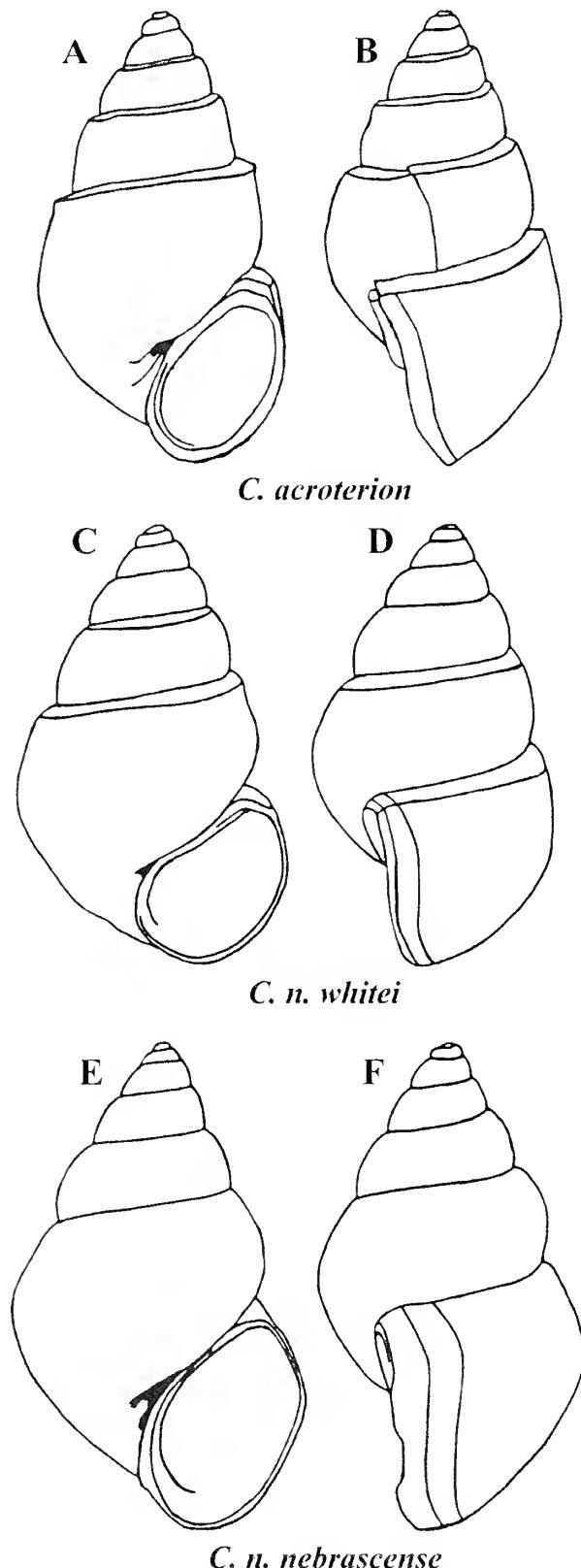
### ***Campeloma acroterion* new species**

Figures 3-22

**Diagnosis:** *Campeloma acroterion* is distinguished from other fossil species of *Campeloma* by the regular occurrence of a well-marked revolving shoulder and shelf (Fig. 15) a typical example of shoulder and shelf with defined lip). The shelf is characteristically nearly perpendicular to the axis of coiling (Figure 23), and the shell material forming the shelf and shoulder is very



**Figures 3–22.** *Campeloma acroterion* new species. All specimens were coated with ammonium chloride for photography. 3–6. USNM-PAL 374598 [UND-JHH S0942], holotype (L1151); 3. apertural. 4. right lateral. 5. Basal. 6. abapertural. 7–10. USNM-PAL 374600 [UND-JHH S0945], paratype-b (L1151). 7. Apertural. 8. right lateral. 9. Basal. 10. abapertural. 9–12. USNM-PAL 374601 [UND-JHH S0946], paratype-c (L1151). 11. apertural. 12. right lateral. 13. Basal. 14. abapertural. 13–16. USNM-PAL 374599 [UND-JHH S0943], paratype-a (L1151). 15. Apertural. 16. right lateral. 17. Basal. 18. abapertural. 19. UMPC 13602 [UND-JHH S0953], paratype-d (L1151). 19. apertural. 20. UMPC 13603 [UND-JHH S0961], paratype-e (L1151). 20. apertural. 21, 22. UCMP 37428, paratype-f (L1151). 21. Apertural. 22. basal.



**Figure 23.** Outline comparison of *Campeloma* species (each pair representing apertural and right lateral views; not to scale). **23A, B.** *C. acroterion* (L0053, S0217). **23C, D.** *C. nebrascense whitei* (L0349, UMPC 13609). **23E, F.** *C. nebrascense nebrascense* (L0023, UMPC 13604).

much thickened. Shouldering, with tendencies towards shelf development, are common in Paleocene specimens of *C. nebrascense*, exemplified by those specimens assigned to *C. n. whitei*. This subspecies is slightly larger than *C. acroterion* and characteristically has a more sloping shoulder (Figure 23), which is also more variably expressed within a population.

**Description:** Shells medium in size, commonly ranging from 25 to 30 mm in maximum height, a few fragmentary specimens indicate the species might attain heights of up to 35–40 mm (Table 2); maximum number

**Table 2.** *Viviparus acroterion*. Measurement Summary (in mm).

MEASURE	N	MEAN	SD	MIN	MAX
#W	14	6.6	0.3	5.7	6.9
MSA	14	52	3.2	46.5	56.5
PHI	7	24.6	2.8	22.6	30.6
PWI	7	14.9	1.2	13.4	16.9
PSH1	8	8.5	1.4	7.5	11.6
PBH	8	16.4	1.6	15.0	19.6
PSW1 (MSW)	14	13.4	1.6	9.1	15.6
PSH2 (MSH)	14	12.7	2.0	7.8	16.1
FAH	11	11.9	1.6	9.1	13.9
FAW	11	8.8	1.4	6.3	10.9
MSW/MSH	14	1.06	0.07	0.93	1.16

**Table 3.** Stratigraphic distribution of *Campeloma acroterion* (examined specimens only).

Stratigraphic Unit State/Province	Localities (Lnos)
Ravenscrag Formation	
Saskatchewan	L0220, L0436
Ludlow Member, Fort Union Formation	
North Dakota	L0184?, L0185?
Lebo Member, Fort Union Formation	
Montana	L1412(LE?), L1420(LE?)
Tullock (Bear) Member, Fort Union Formation	
Montana	L0128
Tullock Member, Fort Union Formation	
Montana	L0010B, L0027, L0902(TU?), L0924, L0925, L2951
Hell Creek Formation	
Montana	L0017A, L0020, L0021, L0053, L0182, L0419?, L0560B, L0586A, L5087?, L1147, L1149?, L1150, L1151 <sup>1*</sup> , L1152, L1153, L1356, L1415, L2373, L2949, L3960, L4321
North Dakota	L0155, L0157, L0158, L0159?, L0162, L0163, L0164?, L0167?, L0169?, L0170?, L0175, L0183?, L0923
Lance Formation	
Wyoming	L552B, L734, L735?, L738, L744, L880, L3483, L3486?, L4289, L4292, L4296, L4298, L4299

Code: ? = Questioned identification based on inadequate preservation. (FM?) = Uncertain formational assignment.

\*Type locality.

of whorls observed 7.4, with many specimens greater than 6.2 whorls; measurements below are for "mature" specimens greater than or equal to 6 whorls; average width-to-maximum height ratio 0.60 (1 SD = 0.03, min. = 0.55, max. = 0.64, n = 7, loc. = 3); shell wall thickness variable, ranging from relatively thin to robust; robustness accentuated by substantial thickening on shoulders; apical tip frequently broken. Shells turbiniform, subovately to elongately conic, with an average mean spire angle for specimens with a complete apex 51.7° (average 6.7 W; 1 SD = 3.7, min. = 43.5°, max. = 58.0°, n = 21, loc. = 2), and for all specimens greater than 6 whorls 48.6° (1 SD = 4.4, min. = 38.0°, max. = 58.0°, n = 64, loc. = 6); spire elevated, with an average mean spire width to mean spire height ratio of 1.04 (average of 6.6 W; 1 SD = 0.07, min. = 0.93, max. = 1.14, n = 12, loc. = 2); average spire height-to-body height ratio 0.51 (1 SD = 0.04, min. = 0.47, max. = 0.59, n = 8, loc. = 3); apical tip rounded, teloconch whorls moderately convex, basal periphery rounded; suture moderately impressed, accentuated by strongly developed shoulder and shelf. Growth lines opisthocyst, weakly sigmoidal, finely to moderately developed, with minimal coarsening with increasing shell size. Surface sculpture of multiple revolving lirae and some striae, varying from weakly to finely developed, with the greatest density of lines just below (abapical) whorl periphery; striae, as revolving lines of closely spaced punctae and later as grooves, precede revolving lirae on some specimens; shouldering is preceded by one or two revolving lirae; a pair of lirae often define the shoulder, with the area between the lirae becoming much thickened and accentuated, producing a shelf approximately perpendicular to coiling axis; shelf sometimes with a revolving trough, which can be defined by revolving lirae and striae; a revolving shallow sinus can also occur abapical to the shelf; when the shelf is more oblique to the axis of coiling, its appearance is as a well-defined, usually rather angular, lip. Umbilicate; as a narrow, but well defined opening. Aperture ovate, parietal wall relatively thin; average aperture width to height ratio measured in plane of aperture 0.75 (1 SD = 0.02, min. = 0.69, max. = 0.78, n = 9, loc. = 2), measured in plane of coiling axis 0.79 (1 SD = 0.03, min. = 0.72, max. = 0.86, n = 14, loc. = 3), with a foreshortened change in aperture height of about 8%. Individual specimen measurements are given in Appendix 2 (for graphs of parameters, see Hartman, 1984).

**Etymology:** *acroterion* (Greek), a promontory; as in a projection or extremity; here used in reference to the development of a well-defined shelf.

**Type Specimens:** Holotype, USNM-PAL 374598 (UND-JHH S0942); paratype-a, 374599 (UND-JHH 0943); paratype-b, 374600 (UND-JHH S0945); paratype-c, USNM-PAL 374601 (UND-JHH S0946); paratype-d, UMPC 13602 (UND-JHH S0953); paratype-e, UMPC 13603 (UND-JHH S0961); paratype-f, UCMP 37428;

all from Locality L1151 (see Type Locality and Appendix 1, Locality Register), Hell Creek Formation, Garfield County, Montana.

**Chresonyms—Nomenclatural Summary:** Specimens assigned to this taxon were most frequently identified either as *Campeloma nebrascense* or *C. n. whitei* (see Previously Illustrated Specimens and Appendix 2 for examples of previous identifications).

**Previously Illustrated Specimens now assigned to *C. acroterion***

Figured specimen, USNM-PAL 9029a (L3340)

1883b White, pl. 28, fig. 4a (line drawing) [figured as *C. multilineata* and herein identified as *C. acroterion*?].

Figured specimen, USNM-PAL 9029b (L3340)

1883b White, pl. 28, fig. 4b (line drawing) [figured as *C. multilineata* and herein identified as *C. acroterion*?].

1883d White, pl. 27, fig. 7 (redrawing of White, 1883b) [reidentified as *C. nebrascense whitei* by Russell (1931a) and affirmed by Tozer (1956)].

Figured specimen, GSC 38365 (L0436)

1974 Russell, p. 48, 49, figs. 4a, b [figured as *C. n. whitei*]; figured specimen, UMPC 12432 (L0010b).

1976 Hartman, pl. VII, figs. 10, 11 (unpublished Master's Thesis) [figured as *C. n. whitei*].

Figured specimen, UMPC 12434 (L0027)

1976 Hartman, pl. VII, fig. 12 (unpublished Master's Thesis) [figured as *C. n. whitei*].

Figured specimen, UMPC 12433 (L0027)

1976 Hartman, pl. VII, fig. 15 (unpublished Master's Thesis) [figured as *C. n. whitei*].

Figured specimen, UMPC 12435 (L0020)

1976 Hartman, pl. VII, fig. 13 (unpublished Master's Thesis) [figured as *C. n. whitei*].

Figured specimen, USNM-PAL 374598 (L1151)

1984 Hartman, pl. 1, figs. 1–4 (unpublished Ph.D. Dissertation) [figured as holotype of *C. acroterion*].

Figured specimen, USNM-PAL 374600 (L1151)

1984 Hartman, pl. 1, figs. 5–8 (unpublished Ph.D. Dissertation) [figured as paratype-b of *C. acroterion*].

Figured specimen, USNM-PAL 374601 (L1151)

1984 Hartman, pl. 1, figs. 9–12 (unpublished Ph.D. Dissertation) [figured as paratype-c of *C. acroterion*].

Figured specimen, USNM-PAL 374599 (L1151)

1984 Hartman, pl. 1, figs. 13–16 (unpublished Ph.D. Dissertation) [figured as paratype-a of *C. acroterion*].

Figured specimen, UMPC 13602 (L1151)

1984 Hartman, pl. 1, figs. 17 (unpublished Ph.D. Dissertation) [figured as paratype-d of *C. acroterion*].

Figured specimen, UMPC 13603 (L1151)

1984 Hartman, pl. 1, figs. 18 (unpublished Ph.D. Dissertation) [figured as paratype-e of *C. acroterion*].

Figured specimen, UCMP 37428 (L1151)

1984 Hartman, pl. 1, figs. 19, 20 (unpublished Ph.D. Dissertation) [figured as paratype-f of *C. acroterion*].

**Type Locality (L1151):** The type locality was discovered by Harley Garbani (Los Angeles County Museum) as part of the search for dinosaurs and mammals in Hell Creek country. J.H. Garbani and N.T. Greenwald collected a specimen of the type series of *Campeloma acroterion* from "Harley's shell bed" on July 7, 1976 (paratype-f, UCMP 37428; field number – JDA-76-7/7-4; UCB locality number – D-7274). The author was given directions to the locality by Garbani and studied and collected the holotype, paratypes, and measured specimens on: 1979 (July 26–27, UM; paratype-a, b, c, d, e); 1982 (July 26, Hartman, UM; holotype); 1991 (July 20; Hartman, W.D. Peck, and D.E. Heinen, UND); 2002 (July 18; Hartman; R. Mattison, Wellesley College; S. Uthus, UND); and 2008 (July 22; A.E. Bogan, D.P. McCollor, UND-EERC; K. Voegele, Concordia College; and others).

Locality L1151 occurs in the East Ried Coulee unit (see Hartman et al., 2014) of the Hell Creek Formation at approximately 27.4 m (90 ft) (Hartman, 1998) below the Z coalbed (after Archibald, 1982) that approximates the top of the formation with the overlying Tullock Member of the Fort Union Formation (Hartman et al., 2014). The locality is at an elevation of about 823 m (2700 ft) on a north-trending promontory, near the center of the south edge of the NW $\frac{1}{4}$  SW $\frac{1}{4}$  NE $\frac{1}{4}$  sec. 5, T. 20 N., R. 37 E., Trumbo Ranch Quadrangle (1971), Garfield County, Montana (see map, Figure 24).

**General Distribution:** Recognizably distinctive specimens of *Campeloma acroterion* are found throughout the Lance and Hell Creek Formations in the northern Great Plains (Figure 24). Specimens are frequently a quantitatively important element of the faunule and are often the dominant gastropod. Similar specimens, with distinctively shelled and shouldered whorls, also occur in the overlying Fort Union (Tullock, Bear, and lower Ludlow Members [Tullock Formation after others and Frye, 1967]) and basal Ravenscrag Formations. The poorly preserved specimens previously reported from the upper part of the Livingston Group of the Crazy Mountains Basin of south-central Montana are now reassigned to horizons within the Hell Creek and Fort Union Formations (Table 3; revised from Hartman, 1984, table 24).

Uppermost Cretaceous records from the Hell Creek Formation in Custer, Dawson (or Wilbaux), Garfield, Golden Valley, Meagher, McCone, Rosebud, Wibaux (or Dawson), and Yellowstone Counties, Montana; from Bowman, Emmons, Grant, Morton, Sioux, and Slope

Counties, North Dakota; from the Lance Formation in Niobrara County, Wyoming; from the Paleocene Fort Union Formation members including the Bear Member in Wheatland County, Montana; from the Tullock Member in Daniels, Garfield, and McCone Counties, Montana; with uncertainty from the Lebo Member in Wheatland County; from the Ludlow Member in Slope County, North Dakota; and from the Ravenscrag Formation in Cypress Hills in southernmost Saskatchewan. Cadastral location data for examined *C. acroterion* are given in Hartman (1984, table 25).

Frye (1967, 1969) lithostratigraphically organized the Hell Creek Formation into several members. Identification of Frye's (1967) specimens shows *C. acroterion* to occur in the Pretty Butte (L0183?), Huff (L0170?, L0175), and Fort Rice (L0155, L0157, L0158, L0159?, L0162, L0163, L0164?, L0167?, L0169?) members. Carlson (1979; personal communication, 15 June 1981), Murphy et al. (2002), and others questioned the utility and ability of others to recognize these subdivisions. Butler (1980), Butler and Hartman (1999), Lund et al. (2002) and Hartman et al. (2014) suggested that a Hell Creek Formation architecture exists and could be correlated in both surface exposures and subsurface logs. The member contacts proposed by Frye (1967, 1969) may not be as useful as he hoped, but his lithofacies have been recognized significantly beyond the limits of their type sections (Butler, 1980; Hartman et al., 2014).

#### Subfamily Viviparinae Gray, 1847

##### *Viviparus* Montfort, 1810

**Etymology:** *viviparus*, that brings forth its young alive.

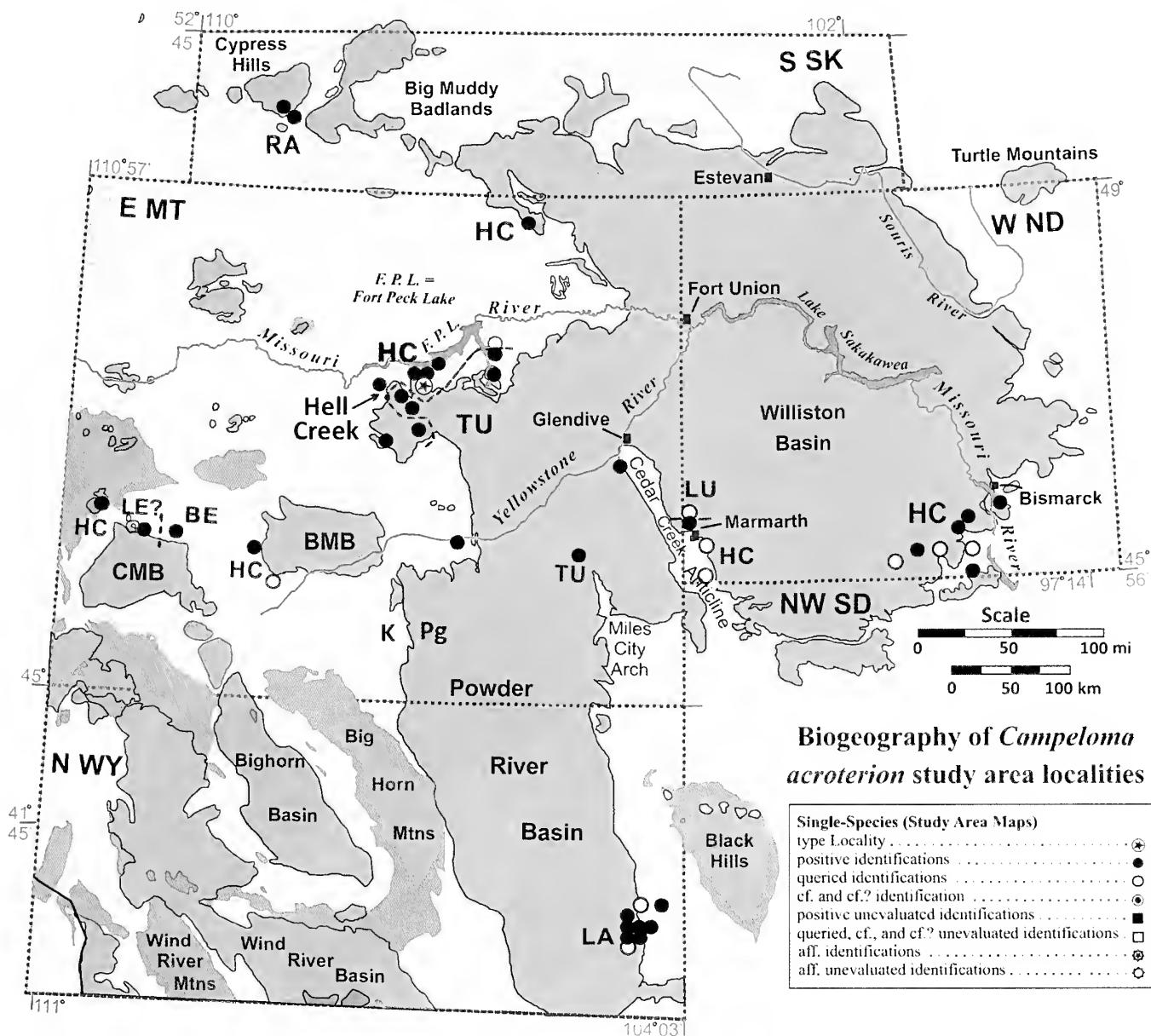
**Type Species:** *Viviparus fluviorum* Montfort, 1810 (= *Helix vivipara* Linnaeus, 1758) (available, see ICZN, 1959, Opinion 573).

##### *Viviparus purgatorius* new species

Figures 25–66

**Diagnosis:** *Viviparus purgatorius* is distinguished from other fossil Viviparinae on the basis of a suite of characters including a much greater mean spire angle, much more inclined growth lines, strongly keeled and crenulated periphery (in adult specimens), and development of nodes in adult forms. Only *V. retusus* growth lines are as acutely inclined to the periphery, but it differs from *V. purgatorius* in being much smaller in size for the same number of whorls, in possessing a depressed spire, and in lacking significant sculpture (compare selected *Viviparus* morphologies, see Figure 67).

*Viviparus formosus* resembles *V. purgatorius* in maintaining a large mean spire angle for a large shell size, but it differs from *V. purgatorius* in possessing less inclined growth lines, and a more elevated spire, in lacking nodes, and in lacking a crenulated, strongly angular basal periphery. *Viviparus* sp. form-W also resembles *V. purgatorius* in maintaining a large mean spire angle



**Figure 24.** Biogeography of *Campeloma acroterion* localities in the northern Great Plains and intermontane basins of the USA and Canada. Upland areas (roughly Laramide uplifts) are shown in pink, with preserved Paleogene and younger sediments preserved in basins shown in yellow (see Abbreviations.)

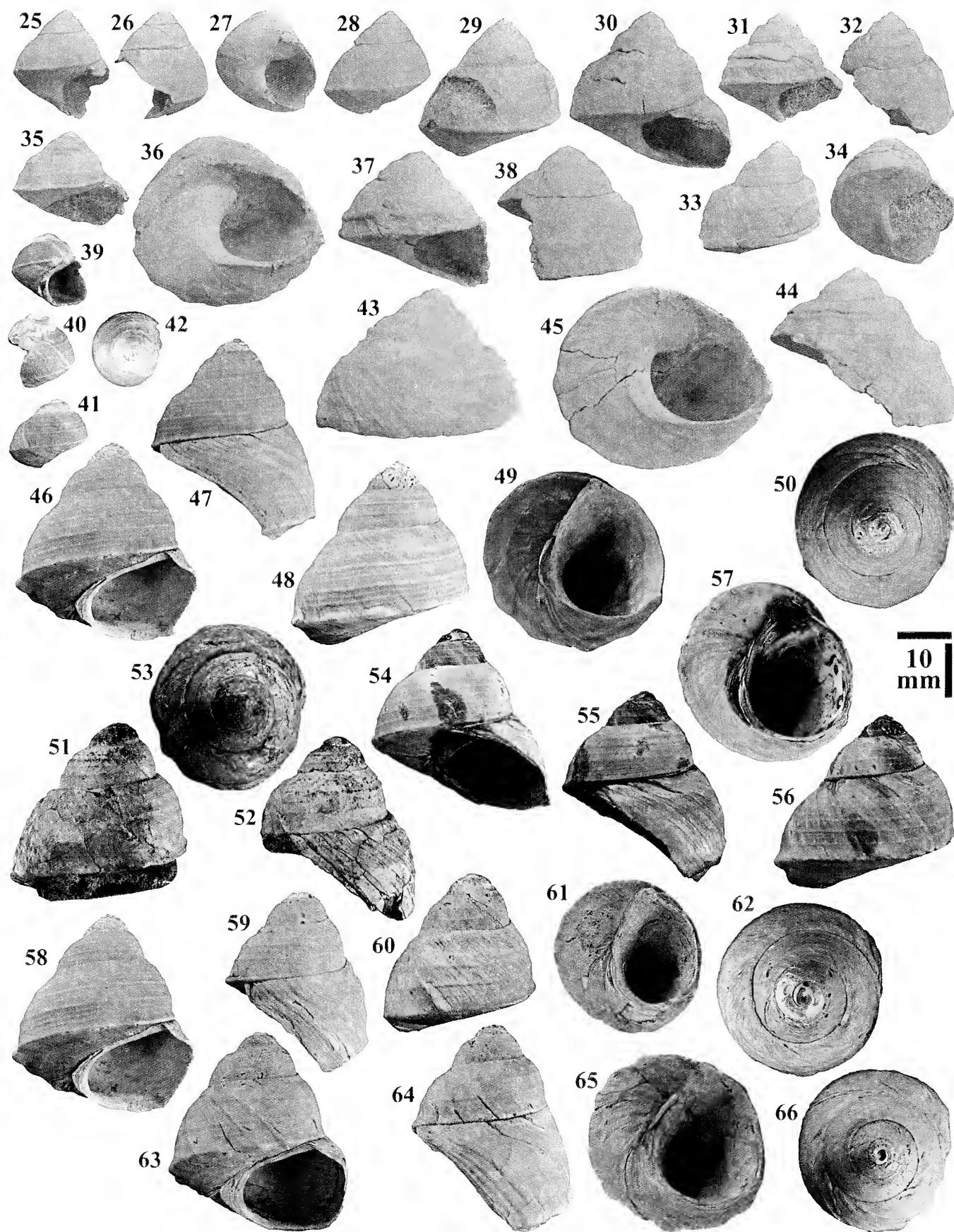
for a large shell size, but differs from *V. purgatorius* most obviously in possessing a much more rounded basal periphery, but also in lacking nodes, a crenulated periphery, and in possessing a larger last whorl expansion ratio.

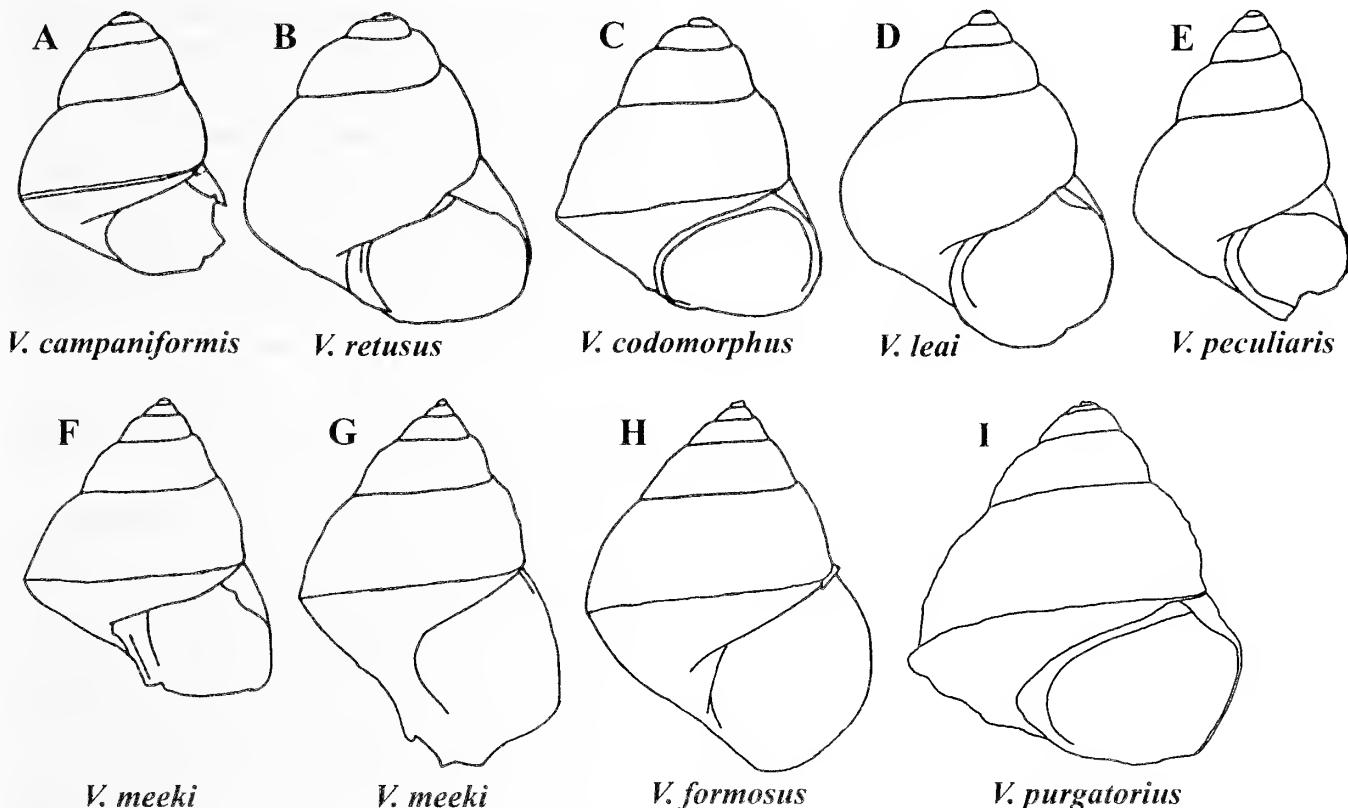
Other noduliferous species proximal to *V. purgatorius* are Paleocene *Viviparus codomorphus* and Cretaceous *V. thompsoni*. *Viviparus codomorphus* differs from *V. purgatorius* in possessing a more blunted apex, in the infrequency of adapical node development (only one specimen has nodes developed), and in lacking a crenulated periphery. *V. thompsoni* differs from *V. purgatorius* in possessing a distinctive pattern of nodes and node ridges. *Viviparus purgatorius* also differs from *V. thompsoni* in lacking any significant basal

surface sculpture (other than spiral lirae) on the latter whorls of larger specimens.

**Description:** When this species was originally recognized and described informally, no undeformed large specimens of this taxon existed, prohibiting a rigorous, numerically calibrated description. Essentially complete, undistorted large specimens were subsequently discovered by D.L. Lofgren (see Appendix 2).

Shells relatively large in size, attaining a maximum height of about 35 mm; maximum number of whorls observed 6.9; measurements given below are for mature specimens from 5 to 6 greater whorls; shell walls relatively thin (Table 4). Shells subtrochiform, globosely





**Figure 67.** Outline comparison of *Viviparus* species (apertural views, not to scale). **67A–C.** Blunted apex. **67A.** *V. campaniformis* (L0070; S0517). **67B.** *V. retusus* (L0435; USNM-PAL 2155). **67C.** *V. codomorphus* (L0049; USNM-PAL 374604). **67D.** Pointed apex, rounded whorls and periphery. **67D.** *V. leai* (L2305; USNM-PAL 2154). **67E–I.** Pointed apex, subtrochiform marginal outline. **67E.** *V. peculiaris* (L0349; S0309). **67F.** *V. meeki* (L0953; USNM-PAL 374985). **67G.** *V. meeki*, narrower form (L0953; USNM-PAL 374986). **67H.** *V. formosus* (L0435; USNM-PAL 2159). **67I.** *V. purgatorius* (L6460, S10441).

conic, with an average mean spire angle of  $68.5^\circ$  ( $\#W \geq 5.5$ : aver  $\#W = 5.7$  W, 1 SD = 9.26, min =  $61.9^\circ$ , max =  $75.0^\circ$ , n = 2, loc = 2;  $\#W \geq 5.0$ : MSA =  $66.6^\circ$ , 1 SD = 5.1, min. =  $61.9^\circ$ , max. =  $73.5^\circ$ , n = 4, loc. = 3;  $\#W \geq 4.6$ : MSA =  $68.8^\circ$ , 1 SD = 6.5, min. =  $81.5^\circ$ , max. =  $60.0^\circ$ , n = 16, loc. = 6); average last whorl expansion ratio of 1.88 (1 SD = 0.03, min. = 1.84, max. = 1.90, n = 4, loc. = 2); apical tip bluntly pointed, apical whorls not substantially produced; teloconch whorls broadly

convex, with an average mean spire width to mean spire height ratio of 3.3 (aver of 5.5 W: 1 SD = 1.00, min. = 1.52, max. = 1.51, n = 6, loc. = 1); spire height-to-body height ratio 0.30 (1 SD = 0.04, min. = 0.22, max. = 0.30, n = 3, loc. = 1); slight adapical shouldering proximal to the suture; upper spire and basal periphery carinate-angular, with basal periphery often strongly angular; suture slightly to very slightly impressed. Growth lines prosocline, very strongly inclined at about  $38^\circ$  ( $\#W \geq 5.0$ :

**Figures 25–66.** *Viviparus purgatorius* new species. Specimens from Localities L0010b and L0214 were coated with ammonium chloride for photography. **25–28.** GSC-IP 76957, hypotype (L0214). **25.** apertural. **26.** right lateral. **27.** basal. **28.** apertural. **29.** GSC-IP 76958, hypotype (L0214). **29.** abapertural (specimen slightly distorted). **30.** UMPC 12427 [UND-JHH S0754], paratype-a (L0010b). **30.** apertural (specimen distorted). **31–34.** USNM-PAL 374614 [UND-JHH S0755], paratype-b (L0010b). **31.** apertural. **32.** right lateral. **33.** abapertural. **34.** basal (specimen slightly distorted, abaperturally depressed). **35.** UMPC 13616 [UND-JHH S0757], paratype-d (L0010b). **35.** apertural. **36.** UMPC 13617 [UND-JHH S1025], paratype-e (L0010b). **36.** basal (specimen distorted). **37, 38.** UMPC 12428 [UND-JHH S0756], paratype-c (L0010b). **37.** apertural. **38.** right lateral. **39–41.** USNM-PAL 374613 [UMPC 12429; UND-JHH S0753], paratype-f (was unpublished holotype) (L0010b). **39.** right lateral. **40.** abapertural. **41.** basal (specimen axially compressed). **42–45.** UND-JHH S10443, figured young specimen, topotype (L6460). **42.** apertural. **43.** right lateral. **44.** abapertural. **45.** apieal. **46–50.** USNM-PAL request1 [UND-JHH S10441], holotype (L6460). **46.** apertural. **47.** right lateral. **48.** Abapertural. **49.** apertural flush. **50.** apical. **51–53.** USNM-PAL will request2 [UND-JHH S10445], paratype-g, topotype (L6460). **51.** apertural. **52.** right lateral. **53.** apical. **54–57.** USNM-PAL request [UND-JHH S10439], paratype-h, (L6460). **54.** apertural oblique. **55.** right lateral. **56.** Abapertural. **57.** apertural flush. **58–62.** UND-PC 16163 [UND-JHH S10446], paratype-I (L6460). **58.** apertural. **59.** right lateral. **60.** abapertural. **61.** apertural flush. **62.** apical. **63–66.** UND-PC 16164 [UND-JHH S10447], paratype-j (L6460). **63.** apertural. **64.** right lateral. **65.** apertural flush. **66.** apical.

**Table 4.** *Viviparus purgatorius*. Measurement Summary (in mm).<sup>1\*</sup>

MEASURE	N	MEAN	SD	MIN	MAX
#W	8	5.7	0.6	5.0	6.9
MSA	6	68.2	5.2	61.9	75.0
MH1	5	35.4	2.2	33.1	38.3
PH1	7	31.5	6.7	18.8	37.1
PWI	10	27.8	5.4	17.3	33.0
PSH1	5	8.3	2.4	5.9	11.4
PBH	5	25.3	1.9	23.3	28.0
PSW1(MSW)	5	25.5	5.3	17.4	32.4
PSW2	5	13.7	3.2	9.3	18.3
PSH2(MSH)	4	18.0	6.5	6.5	26.3
PAH	3	14.2	0.6	13.6	14.8
PAW	3	26.5	12.4	17.8	40.7
FAH	2	24.6	3.2	22.3	26.9
FAW	2	19.9	2.8	17.4	21.3
GLA	4	43.0	10.0	31.0	53.0
MSW/MSH	6	3.3	1.00	1.5	4.5
MSW/PSW2	15	1.9	0.10	1.7	2.1

\*On specimens with  $\geq 5$  #W.

GLA = 41.2°, 1 SD = 10.1, min. = 31.0°, max. = 53.0°, n = 5, loc. = 2; nearly straight, but apparently with a slight adapertural arch proximal to suture; fine-to-moderate development, becoming coarser on latter whorls of larger specimens. Sculpture consists, in part, of a pair of slightly raised revolving ridges of approximately equal prominence and nearly equally spaced between ad- and abapical sutures, strongly reminiscent of some specimens of *V. meeki*; revolving ridges appear to be most clearly seen on upper spire whorls, becoming more obscure with increasing shell height; other revolving lirae may be approximately equal in prominence to the pair of raised ridges, and may thus obscure the basic sculptural similarity with *V. meeki*; Paleogene revolving sculpture is obscure to absent, but some lirae occur below (abapical) basal periphery, are of approximately equal prominence, and are best seen on smaller specimens; a few specimens show a slight, basal surface ridge without nodes; basal periphery keeled and slightly to moderately crenulated on larger specimens, reminiscent of *V. thompsoni*; crenulation may be enhanced by lateral distortion, but its existence, although seeming to be somewhat variable, appears definitely to be a feature of this species. Without umbilicus, with thick inner apertural wall and umbilical area covered by a distinct, relatively wide and thickened columellar callus. Aperture poorly known, ovate, tapers adapically, with a rather strong outer lip angulation at the whorl periphery; parietal lip thins along basal whorl; aperture plane strongly inclined; average aperture width-to-height ratio measured in plane of aperture 0.78 (1 SD = 0.09, min. = 0.9, max. = 2.9, n = 4, loc. = 1), measured in plane of coiling axis 1.62 (1 SD = 0.85, min. = 0.91, max. = 2.86, n = 4, loc. = 1), with a foreshortened change in aperture height of about 48%. Individual specimen measurements are given in Appendix 2 (for graph of parameters, see Hartman, 1984).

**Etymology:** *purgatorius*, named after Purgatory Hill (L0010), McCone County, Montana, the discovery location for the species.

#### Chresonyms—Nomenclatural Summary

1974 *Viviparus formosus* (Meek and Hayden): Russell, p. 46, 47, figs. 3e, f.  
 1976 *Viviparus* aff. *V. thompsoni* White: Hartman, p. 116–119, 176, pl. VII, figs. 1–5 (unpublished M.S. Thesis).  
 1984 *Viviparus purgatorius* Hartman, p. 445–454, pl. 8, figs. 1–24 (unpublished Ph.D. Dissertation).

#### Previously Illustrated Specimens now assigned to *V. purgatorius*

Figured specimen, GSC 38361 (L0224)  
 1974 Russell, p. 46, 47, figs. 3e, f (figured as *V. formosus*).  
 Figured specimen, GSC 76957 (L0214)  
 1984 Hartman, pl. 8, figs. 1–4 (unpublished Ph.D. Dissertation) [figured as *V. purgatorius*].  
 Figured specimen, GSC 76958 (L0214)  
 1984 Hartman, pl. 8, figs. 5, 6 (unpublished Ph.D. Dissertation) [figured as *V. purgatorius*].  
 Figured specimen, UMPC 12427 (L0010b)  
 1976 Hartman, pl. VII, figs. 1, 2 (unpublished Master's Thesis) [figured as *V. aff. V. thompsoni*]  
 1984 Hartman, pl. 8, figs. 7, 8 (unpublished Ph.D. Dissertation) [figured as paratype-a of *V. purgatorius*].  
 Figured specimen, UMPC 12428 (L0010b)  
 1976 Hartman, pl. VII, figs. 4, 5 (unpublished Master's Thesis) [figured as *V. aff. V. thompsoni*]  
 1984 Hartman, pl. 8, figs. 17–20 (unpublished Ph.D. Dissertation) [figured as paratype-e of *V. purgatorius*].  
 Figured specimen, UMPC 12429 (L0010b)  
 1976 Hartman, pl. VII, fig. 3 (unpublished Master's Thesis) [figured as *V. aff. V. thompsoni*]  
 1984 Hartman, pl. 8, figs. 21–24 (unpublished Ph.D. Dissertation) [figured as holotype of *V. purgatorius*].  
 Figured specimen, UMPC 13617 (L0010b)  
 1984 Hartman, pl. 8, figs. 9, 10 (unpublished Ph.D. Dissertation) [figured as paratype-e of *V. purgatorius*].  
 Figured specimen, UMPC 13616 (L0010b)  
 1984 Hartman, pl. 8, figs. 11, 12 (unpublished Ph.D. Dissertation) [figured as paratype-d of *V. purgatorius*].  
 Figured specimen, USNM-PAL 374614 (L0010b)  
 1984 Hartman, pl. 8, figs. 17, 20 (unpublished Ph.D. Dissertation) [figured as paratype-b of *V. purgatorius*].

**Type Specimens:** Holotype, USNM-PAL 611016 (UND-JHH S10441, L6460); paratype-a UMPC 12427 (UND-JHH S0754, L0010b); paratype-b, USNM-PAL

374614 (UND-JHH S0755, L0010b); paratype-c, UMPC 12428 (UND-JHH S0756, L0010b); paratype-d, UMPC 13616 (UND-JHH S0757, L0010b); paratype-e, UMPC 13617 (UND-JHH S1025, L0010b); paratype-f, USNM-PAL 374613 (UMPC 12429, UND-JHH S0753, L0010b); paratype-g, USNM-PAL 611017 (UND-JHH S10445, L6460); paratype-h, USNM-PAL 611018 (UND-JHH S10439, L6460); paratype-i, UND-PC 16163 (UND-JHH S10446, L6460); and paratype-j, UND-PC 16164 (UND-JHH S10447, L6460) from the Tullock Member, Fort Union Formation, McCone County, Montana (see Type Locality and Appendix 1, Locality Register).

**Reference Specimens:** Hypotypes, GSC-IP 76957, 76958, Locality L0214; Ravenscrag Formation, Big Muddy Valley, on Minton map (1974), Saskatchewan.

**Type Locality (L6460):** The type locality of *Viviparus purgatorius* was discovered August 12, 1994 by Donald L. Lofgren (Raymond M. Alf Museum) and the holotype and paratypes-h and -j were collected from the Racetrack Ridge locality on August 12, 1994, by D.L. Lofgren and W.A. Clemens (University of California-Berkeley) (field 94DLL8-12-2, Alf I94161), along with other measured specimens (see Appendix 2). The specimens were subsequently donated to the UND-PC collections. Paratype-i was collected by Hartman on September 16, 1995 (L6460b; [a-e sites were recognized]). Paratype-g was collected on July 27, 2000 by J.H. Hartman, D. Lamb, D.L. Lofgren, A.C. Raser, G.C. Winsinger. These and other specimens were collected from the Tullock Member of the Fort Union Formation about 36.6 m above base of the MCZ coalbed of Lofgren (1995, McGuire Creek Z) representing here the base of the formation, marking the contact with the underlying Hell Creek Formation. The locality is at an elevation of about 742.8 m (2437 ft) in the W½ NW¼ NE¼ sec. 16, T. 21 N., R. 43 E., on the Nelson Creek Bay Quad. (1973) in McCone County, Montana (see map, Figure 68).

**Reference Locality (L0010b):** Discovery location paratypes (a-f) of *Viviparus purgatorius* were collected by R.E. Sloan and J.H. Hartman in 1974 from Purgatory Hill at an elevation of about 751.3 m (2478 ft), located in SE¼ NE¼ SE¼ NW¼ SW¼, sec. 36, T. 23 N., R. 43 E., Bug Creek Quad. (1973), McCone County, Montana. Locality L0010b is located on the north-facing exposures near the top of the butte in a north-south trending channel capped by a sandstone monolith. The channel cut is stratigraphically about 30.5 m above the MCZ coalbed representing the base of the Tullock Member, Fort Union Formation (see also Bell, 1965, measured section E). Locality L0010b is also the a source of late Puerican mammals interpreted to be Pu2-3 NALMA reported by Van Valen and Sloan (1965) and frequently thereafter (see Hartman, 1978; Archibald, 1987; Lofgren, 1995) (see Figure 68).

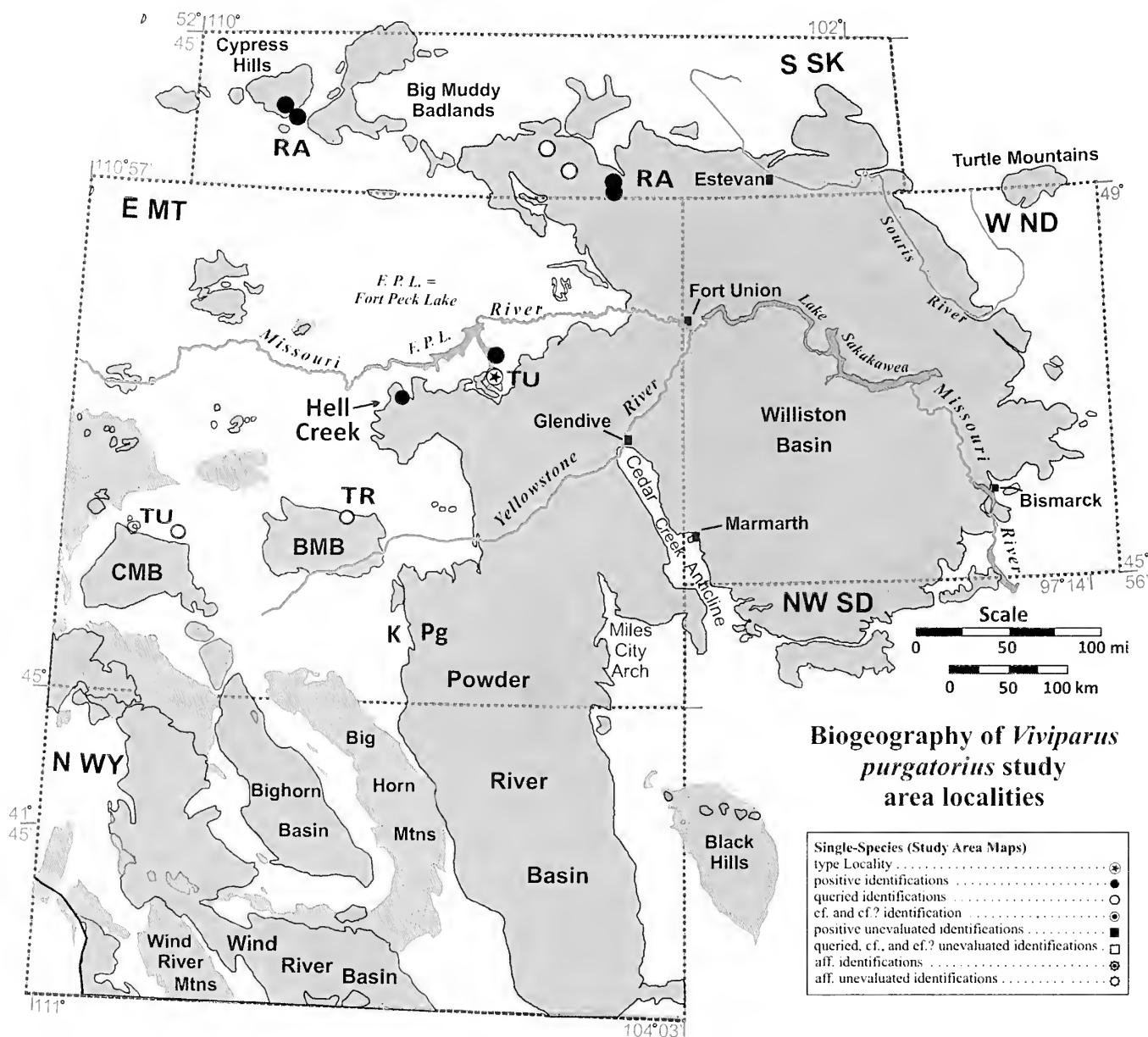
**Literature Distribution:** *Viviparus purgatorius* was reported by Hartman (1976) as *V. aff. V. thompsoni* (see

Chresonyms) from the Tullock Formation in McCone County (L0010b), Montana. The only other previous report of specimens assignable to this taxon were made by L.S. Russell (in Fraser and others, 1935; Russell, 1974) from the Ravenscrag Formation in southernmost Saskatchewan. Russell's identifications, now assigned to *V. purgatorius*, included *V. formosus*, *V. leidyi*, and *V. meeki* (= *V. trochiformis*).

**General Distribution:** *Viviparus purgatorius* was known primarily from distorted and/or incomplete specimens throughout its range in northeastern Montana in the Tullock Member in McCone (L0010b, L0027?) and Garfield (L2951) Counties; southern Saskatchewan in the Ravenscrag Formation (L0209?, L0212?, L0214, L0217?, L0219, L0220, L0223?, L0224, L0225, L0229?, and L0436); and from a queried occurrence in south-central Montana in the Bear Member (Fort Union Formation) in Wheatland County (L0128; see Hartman and Krause, 1993); and from a queried occurrence in the Tongue River Member of the Fort Union Formation in Musselshell County (L1458?) (Figure 68; Table 5) (see Hartman, 1984, table 60 for a cadastral record of occurrences). The record from the Tongue River Member may be referable to *V. meeki*, which, if true, would restrict the age of *V. purgatorius* to early Paleocene (~Pu2-3; L0010b) in Montana. The occurrences of *V. purgatorius* in the Ravenscrag Formation stratigraphically range from a documented early Paleocene locality (Pu2; L0220) in the lower part of the Ravenscrag Formation in the area of Anxiety Butte, to an unresolved Paleocene age in the upper middle part of the formation just above the Willowbunch coal in the Big Muddy Valley area. On the basis of palynological data, Sweet (1978) stated that the strata of the Willowbunch coal zone may be correlative with the Estevan or Boundary coal sequence in the Estevan area, which would probably make the occurrence of *V. purgatorius* in the Big Muddy Valley at least mid Paleocene (Ti2) (see Whitaker and others, 1978, pl. 2, Regional Correlation Sections A-A').

**Discussion – *Viviparus purgatorius*:** Although recognizably distinct, this species was first found plastically deformed. The style of deformation and preservation of Tullock Member and Ravenscrag Formation specimens was very similar suggesting similar shell structure. *V. purgatorius* could be identified on the basis of the features mentioned in the Diagnosis and Description, but the deformed specimen variable whorl convexity, growth line angle, and mean spire angle could make positive identification difficult. The discovery of numerous undistorted specimens at Locality L6460 at Racetrack Ridge confirmed the interpretation of the proposed species (Hartman, 1984) and provided measurements not previously available (Appendix 2).

Probably all of the Ravenscrag Formation specimens identified by Russell (in Fraser and others, 1935; Russell, 1974) as *V. formosus* and *V. leidyi*, and many



**Figure 68.** Biogeography of *Viviparus purgatorius* localities in the northern Great Plains and intermontane basins of the USA and Canada (see Figure 24 for map notes).

**Table 5.** Stratigraphic distribution of *Viviparus codomorphus* (examined specimens only).

Stratigraphic Unit	State	Localities (Lnos)
Fort Union Formation undivided		
Montana		L0936
Ludlow (Upper) (Slope) Member, Fort Union Formation		
North Dakota		L4232A, L4232B
Ludlow Member, Fort Union Formation		
Montana		L0049 <sup>1*</sup> , L0939

\*Type locality; Area interpreted by Vuket et al. (2003) to be Tongue River Member (see text).

identified as *V. meeki* (= *V. trochiformis*), are referable to *V. purgatorius*. The specimens assigned to these younger Paleocene taxa are all very similar and are at once distinguished from *V. purgatorius* by possessing an umbilicus. They also differ in possessing a more pointed apex, less inclined growth lines, and a less angular periphery.

Small and incomplete specimens of *V. purgatorius* could be difficult to separate from either *V. campaniformis* or *V. retusus*, as all three species have a blunt apex and a more or less carinate periphery. Small specimens of these species should not be positively identified unless larger specimens are present in the population. The adult morphologies are, however, quite dissimilar.

**Discussion – *Viviparus* cf. *V. purgatorius*:** All of the specimens assigned to *V. cf. V. purgatorius* are from the Ravenscrag Formation (Localities L0214 and L0218) and appear to represent a morphology distinct from *V. purgatorius*. *Viviparus* cf. *V. purgatorius* differs from *V. purgatorius* in being notably more striate, particularly on the last whorl of larger specimens, in possessing a less angular periphery with increasing shell size, and in having a more impressed suture. They are similar in possessing multispiral lirae on upper spire whorls, in lacking an umbilicus, and in possessing strongly inclined growth lines. All of the larger specimens assigned to *V. cf. V. purgatorius* are lacking apical whorls. *V. leai* is the only other Paleocene viviparid characterized by revolving striae or punctae, but unlike *V. purgatorius*, it is umbilicate.

### *Viviparus codomorphus* new species

Figures 69–92

**Diagnosis:** *Viviparus codomorphus* is distinguished from other fossil Viviparinae on the basis of a suite of characters including its blunted apical tip (Figure 69), absence of an umbilicus, and mean spire angle for a given number of whorls. *Viviparus codomorphus* is also represented by an atypical specimen (Figure 91, UMPC 13611) displaying adapical nodes and a basal surface ridge. Species with similar morphology are *V. campaniformis* and *V. meeki* (see outline comparisons, Figure 67).

*Viviparus campaniformis* differs from *V. codomorphus* in its greater rounding of apical whorls, more flanged and carinate appearance on upper spire whorls, smaller mean spire angle and last whorl expansion ratio in larger specimens, in attaining a greater shell height for the same number of whorls, and somewhat more inclined growth lines. *V. meeki* differs from *V. codomorphus* in having a pointed apex, attaining an equivalent or somewhat smaller size for a greater number of whorls, and in possessing an umbilicus.

**Description:** Shell medium in size, commonly ranges from 23 to 28 mm in maximum height, rarely exceeding 30 mm; maximum number of whorls observed 5.8, with most specimens ranging from 5.0 to 5.5; measurements given below are for “mature” specimens greater than or equal to 5.0 whorls; average width-to-maximum height ratio 0.82 (1 SD = 0.04, min. = 0.72, max. = 0.90, n = 28, loc. = 4); shell walls moderately thick, frequently robust (Table 6). Shells subtrochiform, broadly conic, with an average mean spire angle for specimens with a complete apex of 62.0° (average of 5.4 W; 1 SD = 3.0, min. = 56.5°, max. = 71.0°, n = 26, loc. = 5), and for all specimens greater than 5.0 whorls of 60.5° (1 SD = 3.3, min. = 53.5°, max. = 71.0°, n = 46, loc. = 5); spire somewhat elevated, with an average mean spire width to mean spire height ratio of 1.34 (average of 5.4 W; 1 SD = 0.08, min. = 1.25, max. = 1.54, n = 22, loc. = 5); last whorl expansion ratio of 1.65 (1 SD = 0.06, min. = 1.54, max. =

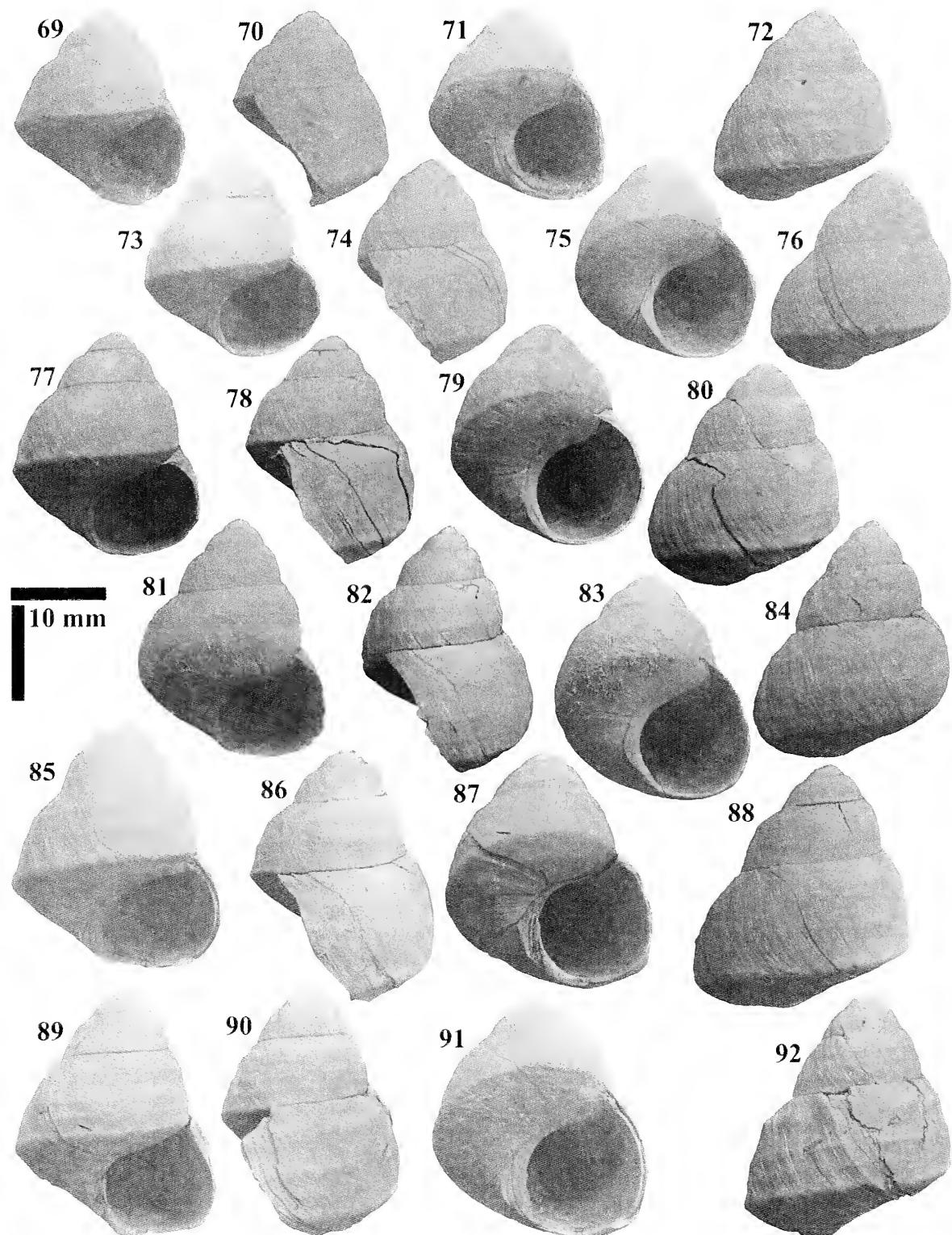
1.80, n = 46, loc. = 5); spire height-to-body height ratio 0.38 (1 SD = 0.06, min. = 0.28, max. = 0.48, n = 30, loc. = 5); apical tip slightly blunted, rounded at extreme tip, teloconch whorls broadly convex, with a slight but consistent oblique shoulder proximal to suture; upper spire whorl periphery angular and carinate, becoming more subangular with increasing shell size, but usually maintaining evidence of a peripheral keel; suture slightly to moderately impressed. Growth lines prosocline, with an average growth-line angle of about 23° (approximately determined: mean = 22.7°, 1 SD = 4.2, min. = 15.0°, max. = 31.0°, n = 25, loc. = 5); nearly straight across midwhorl, although frequently with a slight adapertural arch and usually curved over slight shoulder proximal to suture; finely to moderately developed, becoming somewhat more coarse with increasing shell size. Sculpture consists of a pair or more of slightly raised ridges and very obscure to absent secondary revolving lirae and striae; peripheral carina on upper spire, often accentuated by a slightly adapical revolving stria; revolving sculpture below whorl periphery apparently rare or absent; on one specimen (not obviously developed on any others) with particularly well-developed sculpture, low elongate nodes are developed on the adapical spiral ridge and are expressed only on the last third of the last whorl of 5.5 whorl specimens; node axes appear to parallel the revolving ridge; on the basal surface of the same specimen, one rather wide nodular ridge is developed. Without umbilicus, umbilical area covered by a thickened, but not wide, columellar lip. Aperture broadly ovate, tending towards subquadrate depending on the degree to which the peripheral angularity is expressed on the outer lip; parietal lip not appreciably thinned; average aperture width-to-height ratio measured in plane of aperture 0.89 (1 SD = 0.04, min. = 0.83, max. = 0.99, n = 28, loc. = 4), measured in plane of coiling axis 1.20 (1 SD = 0.11, min. = 1.04, max. = 1.45, n = 28, loc. = 4), with a foreshortened change in aperture height of about 29%. Individual specimen measurements are given in Appendix 2 (for graphs of parameters, see Hartman, 1984).

**Etymology:** *codomorphus* (Greek), codono (kodon), bell; morpho (morphe), form, shape; the shape of a bell.

**Type Specimens:** Holotype, USNM-PAL 374602 (UND-JHH S0892); paratype-a USNM-PAL 374602 (UND-JHH S0200); paratype-b, USNM-PAL 374602 (UND-JHH S0202); paratype-c, USNM-PAL 374606 (UND-JHH S0894); paratype-d, UMPC 13610 (UND-JHH S0900); and paratype-e, UMPC 13611 (UND-JHH S0984) are all from Locality L0049 (see Type Locality and Appendix 1, Locality Register), Tongue River Member (after Vuke et al., 2003; Ludlow Member after Hartman, 1993; and suggested herein) of the Fort Union Formation, Fallon County, Montana.

### Chresonyms–Nomenclatural Summary

1921 *Viviparus (Paludotrochus) trochiformis*: Cossmann, pl. V, figs. 1, 2.



**Figures 69–92.** *Viviparus codomorphus* new species. All specimens were coated with ammonium chloride for photography. 69–72. UMPC 13610 [UND-JHH S0900], paratype-d (L0049). 69. apertural. 70. right lateral. 71. Basal. 72. abapertural. 73–76. USNM-PAL 374603 [UND-JHH S0200], paratype-a (L0049). 73. apertural. 74. right lateral. 75. basal. 76. abapertural. 77–80. USNM-PAL 374605 [UND-JHH S0894], paratype-c (L0049). 77. apertural. 78. right lateral. 79. basal. 80. abapertural. 81–84. USNM-PAL 374602 [UND-JHH S0892], holotype (L0049). 81. Apertural. 82. right lateral. 83. basal. 84. abapertural. 85–88. USNM-PAL 374604 [UND-JHH S0202], paratype-b (L0049). 85. apertural. 86. right lateral. 87. basal. 88. abapertural. 89–92. UMPC 13611 [UND-JHH S0984], paratype-e (L4232). 89. Apertural. 90. right lateral. 91. Basal. 92. abapertural (note node development on basal periphery).

**Table 6.** *Viviparus codomorphus* Measurement Summary (in mm).<sup>1\*</sup>

MEASURE	N	MEAN	SD	MIN	MAX
#W	22	5.3	0.2	4.5	5.8
MSA	22	62.6	3.6	58.0	71.0
MSA	50	61.2	3.6	53.5	71.0
PHI	28	23.1	3.0	13.1	27.6
PWI	28	20.8	2.4	13.0	24.7
PSH1	30	6.4	1.1	3.1	8.1
PBH	30	16.8	2.1	10.1	19.9
PSW1(MSW)	22	17.8	1.8	11.8	20.9
PSW1(MSW)	50	18.4	1.7	11.8	22.4
PSW2	50	11.1	1.2	6.6	13.6
PSH2(MSH)	22	13.3	1.8	7.4	15.4
FAH	28	15.0	1.7	9.6	18.1
FAW	28	13.4	1.6	8.3	16.1
MSW/MSH	22	1.4	0.1	1.2	1.6
MSW/PSW2	50	1.7	0.1	1.5	1.8

\*On specimens with  $\geq 4.5$  #W.

**Table 7.** Stratigraphic distribution of *Viviparus purgatorius* (examined specimens only).

Stratigraphic unit State/Province	Localities (Lnos)
Tongue River Member, Fort Union Formation Montana	L1458?
Tullock (Bear) Member, Fort Union Formation Montana	L0010B, L0027?, L2951, L6460 <sup>1*</sup>
Tullock (Bear) Member, Fort Union Formation Montana (Bear)	L0128?
Ravenscrag Formation Saskatchewan	L0209?, L0212?, L0214, L0217?, L0219, L0220, L0223?, L0224, L0225, L0229?, L0436

Code: ? = Questioned identification based on inadequate preservation.

\*Type locality.

1984 *Viviparus codomorphus* Hartman, p. 331–340, pl. 3, figs. 9–32 (unpublished Ph.D. Dissertation).

#### Previously Illustrated Specimens now assigned to *V. codomorphus*

Figured specimen, repository and locality not known.  
1921 Cossmann, pl. V, figs. 1, 2 (figured as *Viviparus trochiformis*).

Holotype, USNM-PAL 374602 (L0049)  
1984 Hartman, p. 575, pl. 3, figs. 21–24 (unpublished Ph.D. Dissertation) [figured as holotype].

Paratype, USNM-PAL 374603 (L0049)  
1984 Hartman, p. 575, pl. 3, figs. 13–16 (unpublished Ph.D. Dissertation) [figured as paratype-a].

Paratype, USNM-PAL 374604 (L0049)  
1984 Hartman, p. 575, pl. 3, figs. 25–28 (unpublished Ph.D. Dissertation) [figured as paratype-b].

Paratype, USNM-PAL 374605 (L0049)  
1984 Hartman, p. 575, pl. 3, figs. 17–20 (unpublished Ph.D. Dissertation) [figured as paratype-c].

Paratype, UMPC 13610 (L0049)

1984 Hartman, p. 575, pl. 3, figs. 9–12 (unpublished Ph.D. Dissertation) [figured as paratype-d].

Paratype, UMPC 13611 (L4232)

1984 Hartman, p. 575, pl. 3, figs. 29–32 (unpublished Ph.D. Dissertation) [figured as paratype-e].

**Type Locality (L0049):** Mr. Marshall E. Lambert, longtime curator of the Carter County Museum, Ekalaka, Montana, very kindly provided the necessary information and encouragement to relocate a locality he collected in August 1960, but for which he had only vague location information: “North of Baker” locality, 20 to 22 miles [32.2–35.5 km] north of Baker on Highway 7 on a conical butte. The locality was known to locals and the landowner, as it was originally excavated for chicken feed. The location is near the top of a very broad, largely grass-covered, and silcrete-boulder-strewn butte. The specimens were collected from a shallow pit at the north end, now nearly grassed over. The shell-bed thickness is only partially exposed, but is greater than 1-m thick when excavated and may extend over 60 m on a north-south trend.

The type series of *Viviparus codomorphus* was collected on July 8, 1977 by Hartman and J.A. Milske (UM) at an elevation of about 1027 m (3370 ft) from the Shell Butte locality (L0049), located near the center of the NE $\frac{1}{4}$  NE $\frac{1}{4}$  SW $\frac{1}{4}$  sec. 13, T. 10 N., R. 59 E., Shell Butte Quad. (1981), Fallon County, Montana (Figure 93). The locality is mapped as Tongue River Member (Vuke et al., 2003), and is provisionally placed by the author at about 46 m (150 ft) above the top of the underlying Hell Creek Formation. The nearest available exposures of the Fort Union–Hell Creek formalional contact are located about 2 km to the southwest. The exact stratigraphic placement of the locality depends on a more precise knowledge of the amount and change of dip in the strata as the beds flatten to the east on the east flank of the Cedar Creek Anticline. Stratigraphic studies by the author suggest that the locality may actually occur in the Ludlow Member (Hartman, 1993). Vuke et al. (1986) previously mapped the Shell Butte area as FU<sub>3</sub> and correlated it with the Slope Formation of North Dakota. Measured and study specimens were also collected on May 3, 1978, by Hartman, L. Doull, W. Hughes, L. Huntley, A. Krafft, E. Olson, A. Rautman, S. Russell, A. Snodgrass, and M. Timmerman; June 30, 1978, by Hartman and R.C. Holtzman; August 22, 1988, by Hartman; and July 6, 7, 1989, by Hartman, D.W. Krause, T. Kroeger, J. Hunter, G. Buckley, P.P. Lemelin, J.A. Quintana, and K.A. Zarembev.

**Reference Locality (L4232):** Locality L4232 (Brown Ranch locality) was discovered by the author July 28, 1982, and is one of the few continental molluscan localities with abundant snails and/or bivalves that form a shell-layer in the Ludlow Member of the Fort Union Formation in North Dakota. Locality L4232 was found to occur over a significant area of the School Section drainage (L4232a–e) at the same horizon between the

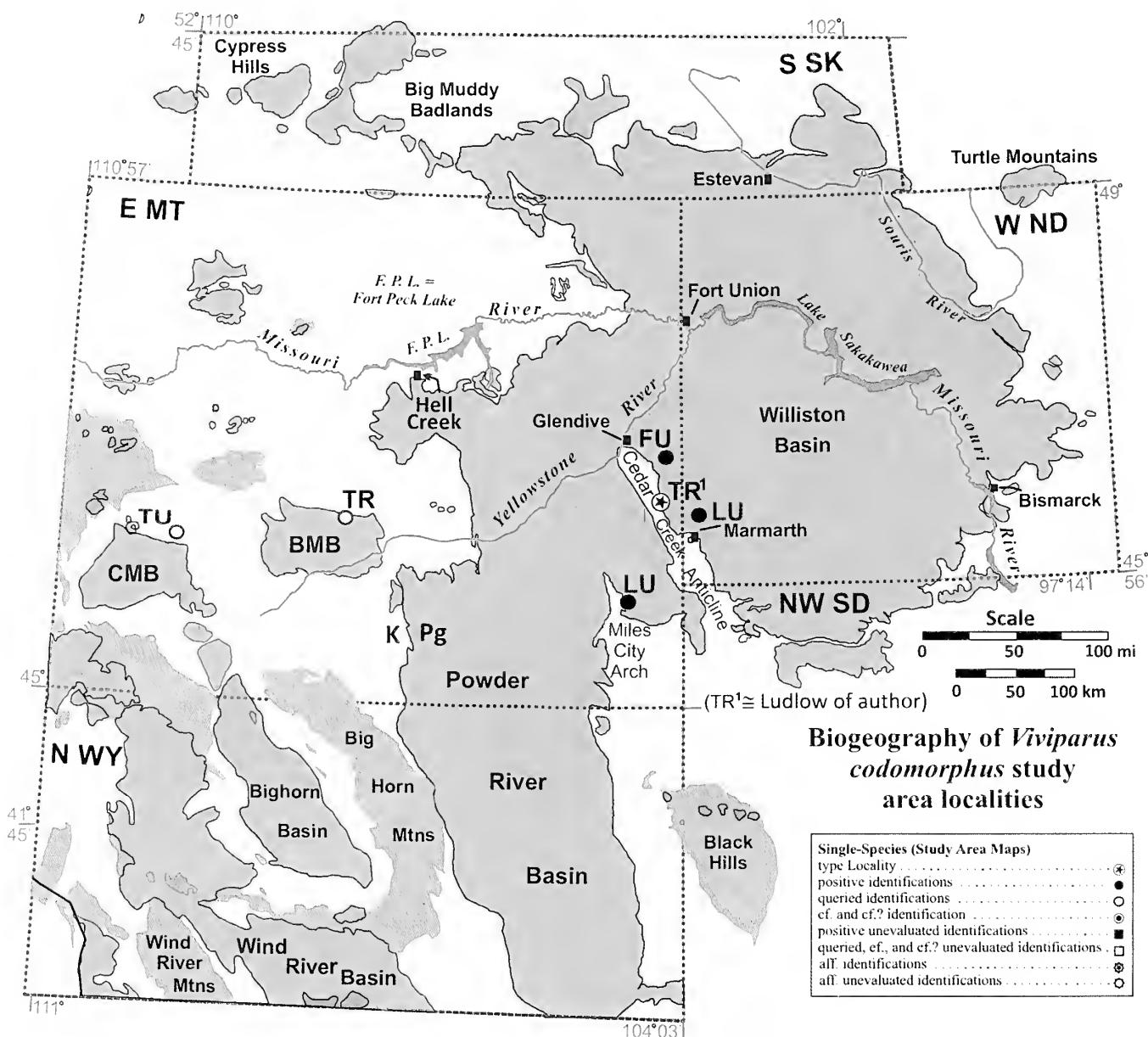


Figure 93. Biogeography of *Viviparus codomorphus* localities in the northern Great Plains of the USA (see Figure 24 for map notes).

“Lower and Upper Coal Pair” and the Boyce and Three V Tongues of the Cannonball Formation (Belt et al., 2005) in the upper part of the Ludlow Member (Slope Formation of others) on the Williams Lake Quad. (1979), Slope County, North Dakota. Measured and other specimens (Appendix 2) were collected at the time of discovery and on July 9, 1986, by Hartman and K.D. Enebo, and others; June 19, 1987, by Hartman, S.G. Strait, R. Crane; and June 23, 1988, by Hartman, D.W. Krause, T.C. Rae, and J.P. Hunter.

**General Distribution:** *Viviparus codomorphus* is presently known from just a few localities. These occurrences may be stratigraphically restricted to the upper part of the Ludlow Member of the Fort Union Formation or may

range into the lowest part of the Tongue River Member (Figure 1; Table 7). All of the occurrences are adjacent to the Cedar Creek Anticline in far-western North Dakota (Slope County, L4232) and easternmost Montana (Carter and Fallon Counties, L0939 and L0049) to the Miles City Arch (Wibaux County, L0936), Montana (see Hartman, 1984, cross section F-8, L4232a, b). This limited distribution is mapped on Figure 93 (see Hartman, 1984, table 42 for cadastral data). Although amenable to bulk processing, no mammal teeth were found at L0049 after considerable effort and pieking. The Brown Ranch local fauna includes mammal teeth from depauperate sites between the Boyce and Three V Tongues of the Cannonball Formation. A To1 or To2 is presently the best age estimate for this interval of the Ludlow Member (Hunter

and Hartman, 2004). The age of the lowermost part of the Tongue River Member in Montana is uncertain, but is unlikely to be younger than Ti2 NALMA (see Figure 1).

#### Discussion – *Viviparus (Paludotrochus) codomorphus*:

*Viviparus codomorphus* is the type species of the genus-group taxon *Paludotrochus* Cossmann. It was introduced to encompass the Late Cretaceous and Paleogene viviparid taxa in the Western Interior (specifically, the Laramie, s.l., of Montana). Cossmann (1921) identified the type species as *Viviparus meeki* (then *V. trochiformis*). However, his description and illustrations clearly indicate that *Paludotrochus* was based on a taxon other than *V. meeki*. Cossmann's description and illustrated specimen are assignable to *V. codomorphus*, thereby recognizing this taxon as the type-species of *Paludotrochus*.

*Viviparus codomorphus* is a relatively uncommon if not rare taxon, but is locally abundant. *V. codomorphus* is presently known only from exposures near the Cedar Creek Anticline in easternmost Montana and westernmost North Dakota (Little Missouri River valley) (Figure 93). Specimens of this species are present in some of the museum collections examined during the course of this study (e.g., GSC general collection). Most museum labels record the following information: Montana (or Dawson County, Montana), Fort Union Formation, Wards. I suggest as a possibility that specimens of this species were acquired by Ward's Natural Science Establishment, Inc., Rochester, New York, and were sold to various institutions and maybe to Cossmann. Interestingly enough, the Ward's specimens were most often identified as *V. trochiformis* (= *V. meeki*).

## DISCUSSION

The Lancian viviparid fauna (Figures 1, 67) is distinctive, but was not recognized so by earlier paleontologists. In the Williston Basin, the Lancian fauna is largely characterized by *C. acroterion* and *V. thompsoni*. The former can occur by the thousands at some locations, while the latter is always relatively few in numbers. Other species of *Viviparus* are also present in the Lancian of Montana and North Dakota and await further treatment. They, too, are also relatively uncommon, with the North Dakota specimens preserved as sideritic steinkerns (Justham et al., 2007).

The Puerian (early Paleocene) viviparid fauna is based on relatively few localities, but additional records are available (with limited temporal control) from studies in the Bear Formation of the Crazy Mountains Basin, Montana (Hartman, 1989). Bear Formation localities are interpreted as lower Paleocene based on mammalian studies by Buckley (Hartman et al., 1989; Buckley, 1995). The discovery of the Raettrack Ridge locality confirmed the distinctiveness of the *Viviparus purgatorius*, and provided an additional local fauna for comparison. Other localities of importance include Purgatory Hill (L0010) in Montana and Pine Cree Park (L0437) in

Cypress Hills, southwestern Saskatchewan, from the basal strata of the Ravenscrag Formation. All of the localities below the Pine Cree Locality are interpreted to be early Paleocene. Locality L0220 occurs in the lowermost strata of the Ravenscrag Formation and is probably the oldest Paleocene locality of this report.

Few Torrejonian viviparid-bearing localities are known from the Williston Basin (Hartman, 1984). The two best-known localities (L0049 and L4232) provide very well preserved specimens of *Viviparus codomorphus* and associated fossils, indicating their distinctiveness. Subsequent work has found a large number of Torrejonian-age localities in the Crazy Mountains Basin. Although most material is plastically deformed, viviparid diversity appears to remain low although specimens are common. Possible occurrences of *Viviparus codomorphus* in the lowermost part of the Tongue River Member may indicate an upper Torrejonian or lower Tiffanian age, depending on location. In Saskatchewan, in the valley of the Big Muddy, the age of the Ravenscrag Formation may be at least mid Paleocene (Ti2) (Sweet, 1978; Craig Scott, Geological Survey of Canada, verbal communication, 2014).

Three new species viviparid species herald the species and evolution to follow in their respective genera. All three species appear to have existed for about the same duration (3 million years). *Campeloma acroterion* is beginning part of a succession of three species of *Campeloma* over about a 12 million-year period that may be traced back to *C. vetula* (Meek and Hayden) of the Campanian Judith River Formation of north-central Montana. *Viviparus purgatorius* and *V. codomorphus* may or may not give rise to the radiation of *Viviparus* taxa seen in the northern Great Plains later in the Paleocene. Viviparid taxa are a common if not dominant macrogastropod element of primarily fluvial faunas during the changes in sea level effecting Laramidia during the Late Cretaceous. The taxa have a similar, if maybe reduced, overall disparity and diversity in early and mid Paleocene faunas with multiple incursions of the Cannonball Sea. With regression of the Cannonball Sea in the early late Paleocene (Hartman et al., 1999), viviparids radiate, becoming far more numerous, diverse, and morphologically variable until the end of the Laramide Orogeny (about mid Eocene). The species introduced here, along with others that may exist, foreshadow the success of *Viviparus* in the late Paleocene in North America.

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# Shell shape variation within a population of *Astarte borealis* (Schumacher, 1817) (Bivalvia: Astartidae) from Camden Bay, northern Alaska: a study using elliptical Fourier analysis

M.E. Chrpa

Department of Geology and Geophysics, MS 3115  
Texas A&M University  
College Station, TX 77843 USA  
mchrpa@tamu.edu

A.O. Oleinik

Department of Geosciences  
Florida Atlantic University  
777 Glades Road  
Boca Raton, FL 33431 USA  
aoleinik@fau.edu

## ABSTRACT

Shells in the bivalve genus *Astarte* are known for variable morphology and polymorphism within living and fossil species. *Astarte borealis* (Schumacher, 1817), the most common living species, is recognizable and common in the mid- to high-latitude North Pacific, Arctic, and North Atlantic oceans, and has been previously subdivided into several subspecies and varieties based on variations in overall shell shape. A collection of 641 recent specimens of *A. borealis* from Camden Bay, northern Alaska, with intact outlines was analyzed for variability of the shell shape within a population of the species. The analysis has important implications for morphological studies of recent and fossil bivalve mollusks. Bivariate analysis of length vs. height and morphometric analysis of shell outline determined variants within a population of *A. borealis*, and were compared to Pliocene *A. borealis*. The computer program SHAPE version 1.3 (Iwata and Ukai, 2002) uses elliptic Fourier coefficients of shell outlines to evaluate and visualize shape variations. The multivariate outline analysis indicates that intraspecific shell variation in *A. borealis* is based upon a modal shape that grades into other shapes, rather than grade between two or more end-forms.

*Additional Keywords:* Multivariate outline analysis

## INTRODUCTION

It has long been suggested that the outlines of objects, mollusk shells in this case, are of great significance to visual recognition and are therefore important for classification purposes (Scott, 1980). The outline measurements, however has not been widely used in taxonomic studies, in favor of more traditional distance measurements of height, length, and width, and relative geometric locations of certain well-defined characters, known as “landmarks”. Part of the problem was the lack of suitable instrumentation for precise outline measurements. Advances in computer technology and digital image analysis have taken outline data collection and process-

ing to a new level. Computer-based techniques of shell shape quantification are particularly important for fossil species, where other diagnostic characteristics, such as those in soft tissues, are unavailable for study. One of the common problems arising from attempts to identify large number of similarly shaped individuals is the recognition of patterns of variability within the population(s) that can be used as a basis for precise taxonomic identification. As a test case for outline shape analysis, we selected the high-latitude bivalve *Astarte borealis*. Recent and Pliocene specimens from Alaska were evaluated. Bivalves of the genus *Astarte* Sowerby, 1816 are also notorious for the conservatism in shell shape that made them particularly suitable for this study (Dall, 1920).

The bivalve genus *Astarte* is known from as early as the Lower Jurassic in northern Siberia (Zakharov, 1970). Recent species of *Astarte* are common in circumpolar panarctic waters and are known for polymorphism (Zettler, 2001). One of the most abundant recent species is *Astarte borealis* (Schumacher, 1817). The species is known to have a high degree of shell shape variability and has been often been called a “species complex”, by various authors owing to numerous subspecies and named varieties (Zettler, 2001, 2002; Ockelmann, 1958; Petersen, 2001). Although there are several synonyms attributed to this polymorphic species, there have been few detailed morphological studies done. Qualitatively, the shell varies from ovate to subtrigonal and quadrangular within the genus. Among other characteristics, these qualitative terms are often found in the descriptions of *Astarte* species (Dall, 1903, 1920; Coan et al., 2000). A more precise definition of the shell shape is necessary in an attempt to better quantify the shape of the shell. One of the ways to examine the amount of variation and evaluate the possible presence of different shape morphs with gradation, for both recent and fossil *Astarte* species, is to use statistical techniques to study shell shape variability.

The objective of this study was to quantitatively determine the degree of morphological variability in shell shape

within a population of recent *Astarte borealis*, from a single location in Arctic Alaska, based on a large sample size. The hypothesis for this study is that a population of extant *A. borealis* in Camden Bay, northern Alaska, shows a high degree of variation in shell outline morphology. The variation is attributed to a central form grading into a range of variants rather than the presence of two or more distinct forms. An unbiased clustering around the central form will indicate that any separation of morphologic forms that could potentially be defined within the population is artificial. Existence of at least two distinct shape "clusters" within the population will be suggestive of quantifiable morphological variability in shell shape. The secondary objective was to compare the results of the outline analysis of modern *A. borealis* to Pliocene *A. borealis* from Alaska. That was done to test how a completely random small sample will compare with our dataset. We had chosen a fossil, instead of recent, subset to make samples both spatially and temporally different.

This is the first comprehensive study of the shell outline variation within a single population of *Astarte borealis* based on a large number of specimens. Although *A. borealis* has been studied in comparison to other *Astarte* species (Gardner and Thompson, 1999; Ockelmann, 1958; Saleuddin, 1965, 1967, 1974; Schaefer et al., 1985; Selin, 2007; Skazina et al., 2013; Zettler M.L., 2002), comparative studies using the shell outline to determine the degree and type of variability within *A. borealis* from the same population have never been attempted. The study is important in demonstrating the potential significance of a new technique for understanding the shell shape variation in recent *A. borealis* and has significant implications for systematic studies of both recent and fossil species.

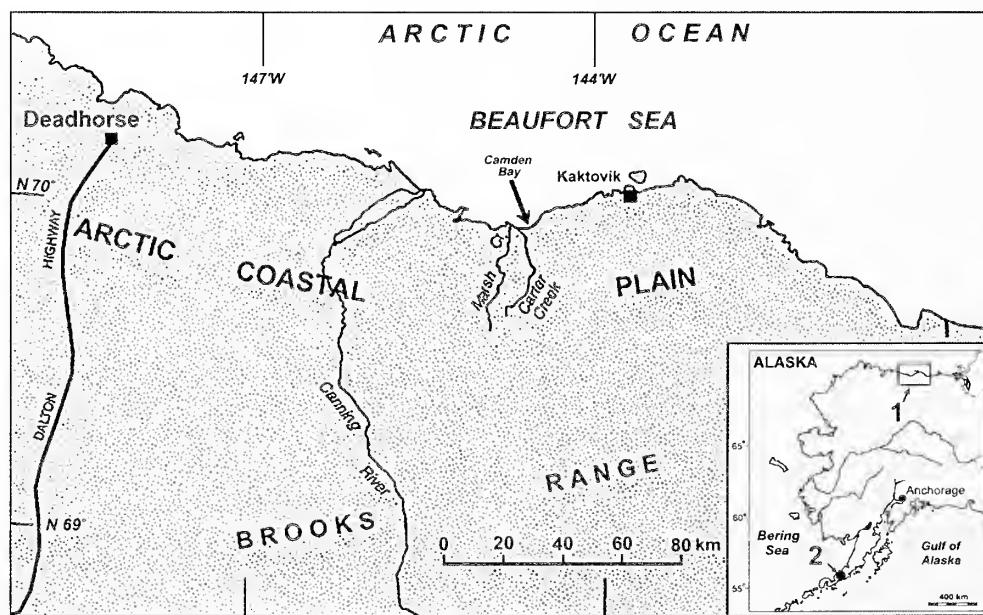
## MATERIALS AND METHODS

More than 700 specimens of recent *Astarte borealis* were collected in July of 2005, along a 5.5 km stretch of gravel beach at Camden Bay, North Slope of Alaska (Figure 1).

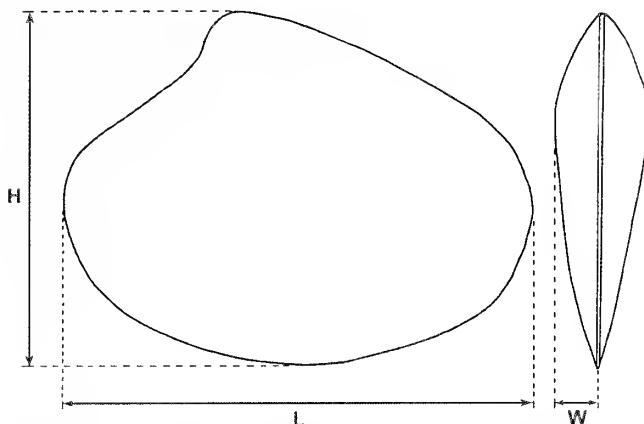
Twenty-three fossil specimens of *Astarte borealis* used in this study were obtained on loan from the California Academy of Sciences, Department of Invertebrate Zoology, and Geology fossil collections. These specimens were collected from the Pliocene marine facies of the Milky River formation at Sandy Ridge section, Alaska Peninsula (Marincovich et al., 2002) (Figure 1). Thirteen specimens from this collection were used for the distance measurement analysis based on completeness with respect to the distance measurements needed. Eleven specimens were used for the outline analysis and were chosen based on degree of outline completeness.

All recent shells were sorted to separate left from right valves, then left valves were retained and sorted again for elimination of specimens without complete outlines. Valves with large chips or partial outlines due to breakage were removed from the study sample. A total of 641 recent left valves and 11 Pliocene specimens were used for this study. Left valves of recent specimens were chosen, with no preference over right valves, to eliminate duplication of a specimen in the quantitative analyses.

All left valves were soaked in 10% sodium hypochlorite solution for approximately 48 hours to remove periostracum, rinsed with de-ionized water, and dried. Fossil specimens were unaltered for this study. Due to limited number of specimens, both left and right valves of fossil *Astarte borealis* were used when complete outline was visible.



**Figure 1.** Map showing location of collection sites in Alaska. 1. Camden Bay, North Slope, recent *Astarte borealis*. 2. Sandy Ridge, Pliocene *A. borealis*.



**Figure 2.** Outline of the shell of *Astarte borealis* showing basic measurements. H: height; L: length; W: width.

Recent shells were prepared for photography by coating the exterior surface with water-based tempera paint to remove any image interference from rust staining on the surfaces. The shells were photographed with digital camera and processed in Adobe Photoshop 7.0 to retain the outline of the image. The fossil shells had no pro-

**Table 1.** Bivariate results for shell proportions of *Astarte borealis* in this study.

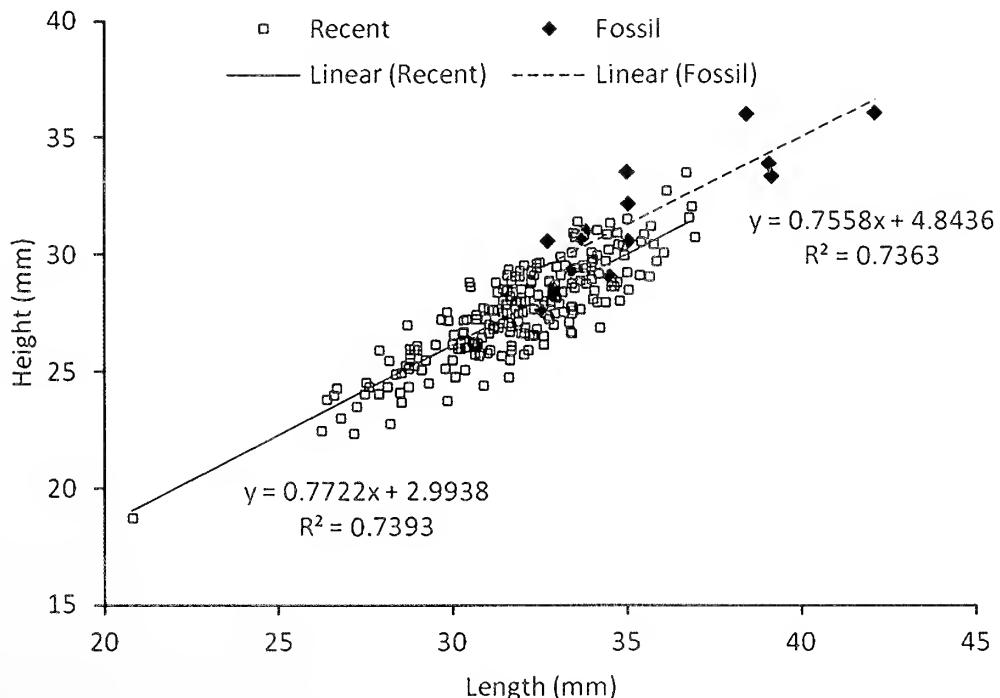
Specimen	L/H	W/H
Recent <i>A. borealis</i>	1.16	0.21
Pliocene <i>A. borealis</i>	1.12	0.24

cessing prior to digital imaging, and images of any right valves were reflected geometrically to represent left valves. The last step was possible due to the equivalence nature of *A. borealis* shell (Saleuddin, 1965).

The length to height (L/H) and width to height (W/H) ratios were calculated for one third of recent specimens that were used for outline analysis. These 225 valves were randomly selected for the distance measurements, as well as 13 fossil specimens. Regarding the measurements, length (L) is the longest distance from front to back edge; height (H) is the distance from the umbo to edge; and width (W), is the longest distance of the valve in a lateral plane across the valve (Figure 2). The linear measurements were taken using a Mitutoyo Absolute Digimatic digital caliper, and were made at a resolution of millimeters to the hundredth place (0.01 mm).

The multivariate outline analysis was performed using SHAPE ver. 1.3, a software package for Quantitative Evaluation of Biological Shapes Based on elliptical Fourier descriptors, developed by Iwata and Ukai (2002). The variation in valve outline shape, a case of a closed contour, is characterized by the Elliptic Fourier descriptors (EFDs), which are obtained by decomposing a curve into a sum of harmonically related ellipses (Kuhl and Giardina, 1982).

First, the chain code was obtained from the processed digital images, using the ChainCoder program (Iwata and Ukai, 2002). The program converts the full color image to black and white by splitting the image into three colors with gray scale, converting the image with clearest contrast to black and white. The noise is reduced and the closed contour of the valve was extracted by edge detection which is described as a chain code. Chain code

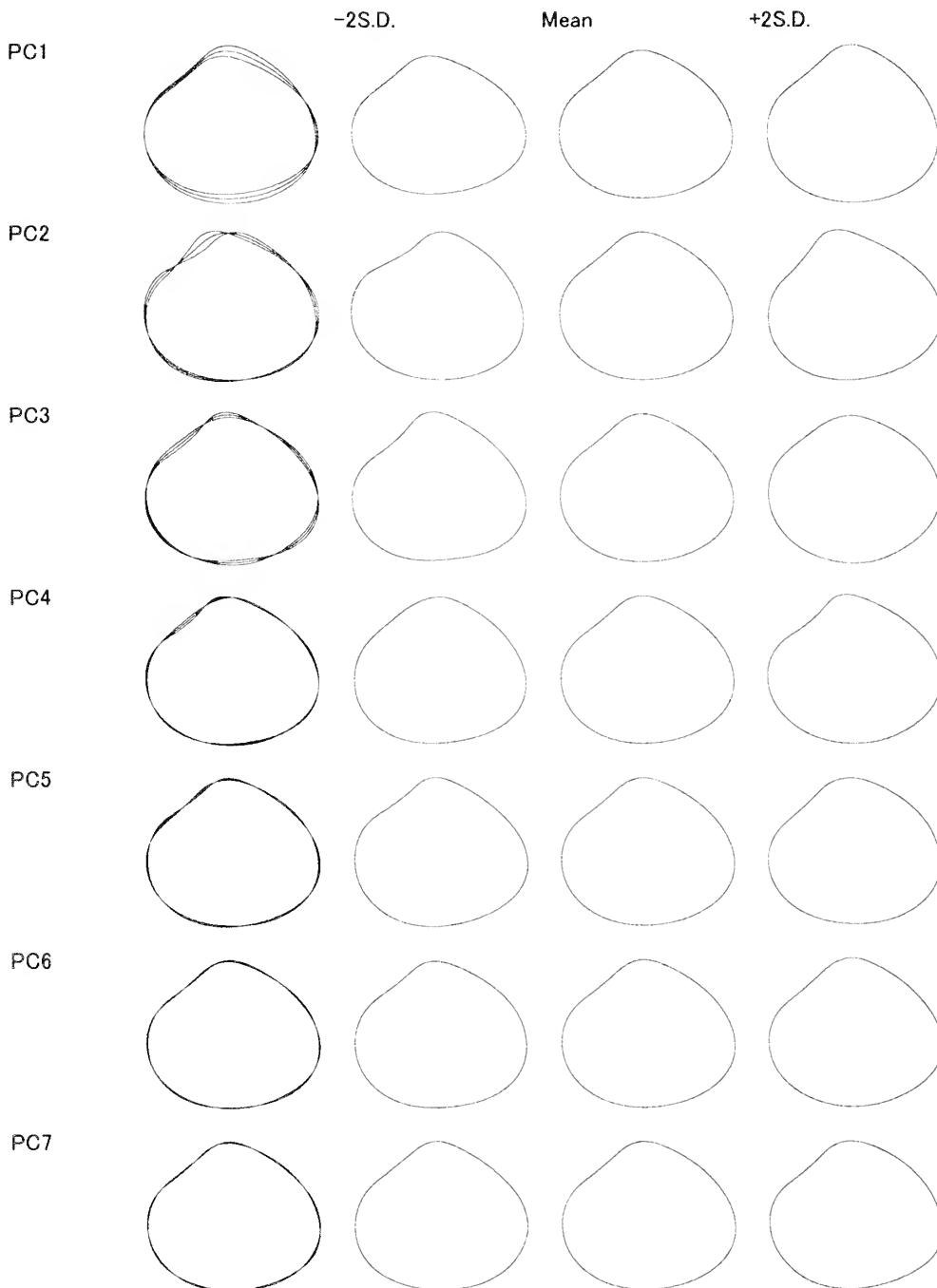


**Figure 3.** H/L relationship for recent and Pliocene shells of *Astarte borealis*.

is a coding system for describing geometrical information about contours using numbers from 0 to 7, indicating direction as measured counterclockwise from X axis of X-Y coordinate system to represent the position of each successive point in relation to the previous (Kuhl and Giardina, 1982). The area of each valve was also recorded.

The normalized Elliptic Fourier descriptors (EFDs) were calculated in Chc2Nef program of the SHAPE ver. 1.3 package (Iwata and Ukai, 2002). The program

obtained chain code to calculate normalized EFDs following the procedures suggested by Kuhl and Giardina (1982). The EFDs are normalized to be invariant with respect to size, rotation, and starting point and are based on the first harmonic ellipse that corresponds to the contour information's first Fourier approximation. The EFDs are used to find the principal components of the shape variation. The principal component analysis of the normalized EFDs was accomplished in the PrinComp program



**Figure 4.** The PrinPrint visualization of the mean shape and the  $+2$  and  $-2$  standard deviation from the mean in outlines for the first 7 significant principal components. The first column shows the outlines of  $+2$  and  $-2$  standard deviation superimposed on the mean form.

of the SHAPE package (Iwata and Ukai, 2002) to efficiently summarize the information contained in these coefficients for easier interpretation. The principal component analysis converts a set of observed correlated variables and by means of orthogonal transformations, produces a set of values that are linearly uncorrelated variables or principal components (Rohlf and Archie, 1984). The first principal component produced has the highest possible variance with respect to the data set. Each successive principal component has the highest possible variance with respect to the preceding component. Principal components were then visualized on a chart.

The visualization of principal component analysis was done through the PrinPrint program. The program outputs the shape variation accounted for by the largest principal components. Following the procedure in Iwata and Ukai (2002), the coefficients of the EFDs are calculated such that the score for a particular principal component is equal to  $+2$  or  $-2$  times the standard deviation from the mean, the square root of the eigenvalue of the particular component and the scores of the remaining components are zero. The coefficients are used to execute an inverse Fourier transform and create contour shapes that are visual representations of the data. That visual output is helpful in interpreting the variation associated with each principal component.

## RESULTS AND DISCUSSION

According to Selin (2007), shell proportions can be a reliable parameter for differentiating between species. The results of bivariate analysis for length to height (L/H) and width to height (W/H) ratios are shown in Table 1.

The L/H ratio is 1.16 and is comparable to the previous result of 1.15 obtained by Zettler (2001), also falling between the ratio of 1.28 obtained by Ockelmann (1958) and 1.10 by Selin (2007). The plot of height and length measurements for both recent and fossil specimens is shown on Figure 3. The correlation coefficient for height to length ratio is  $R^2 = 0.7393$  for the recent (two-tailed P value is less than 0.0001) and  $R^2 = 0.7363$  for the fossil specimens (two-tailed P value equals 0.0027), which suggest a very close similarity of shape between recent and fossil specimens. The outline analysis shows the areas where variability in shell outline was found as well as the proportion of variance that could be attributed to each component of variation among the population. The results of the statistical computation using the SHAPE PrinComp package and the first seven principal components are shown in Figure 4.

Principal components (PC) that represent variance in outline were calculated from the symmetric and asymmetric aspects of the shell. The PrinComp package gives results based numbers of harmonics used in the calculation; for this analysis, 77 principal components were produced. Here, only the first 10 principal components are discussed, as coefficients with small variance and covariance values are generally not important for explaining

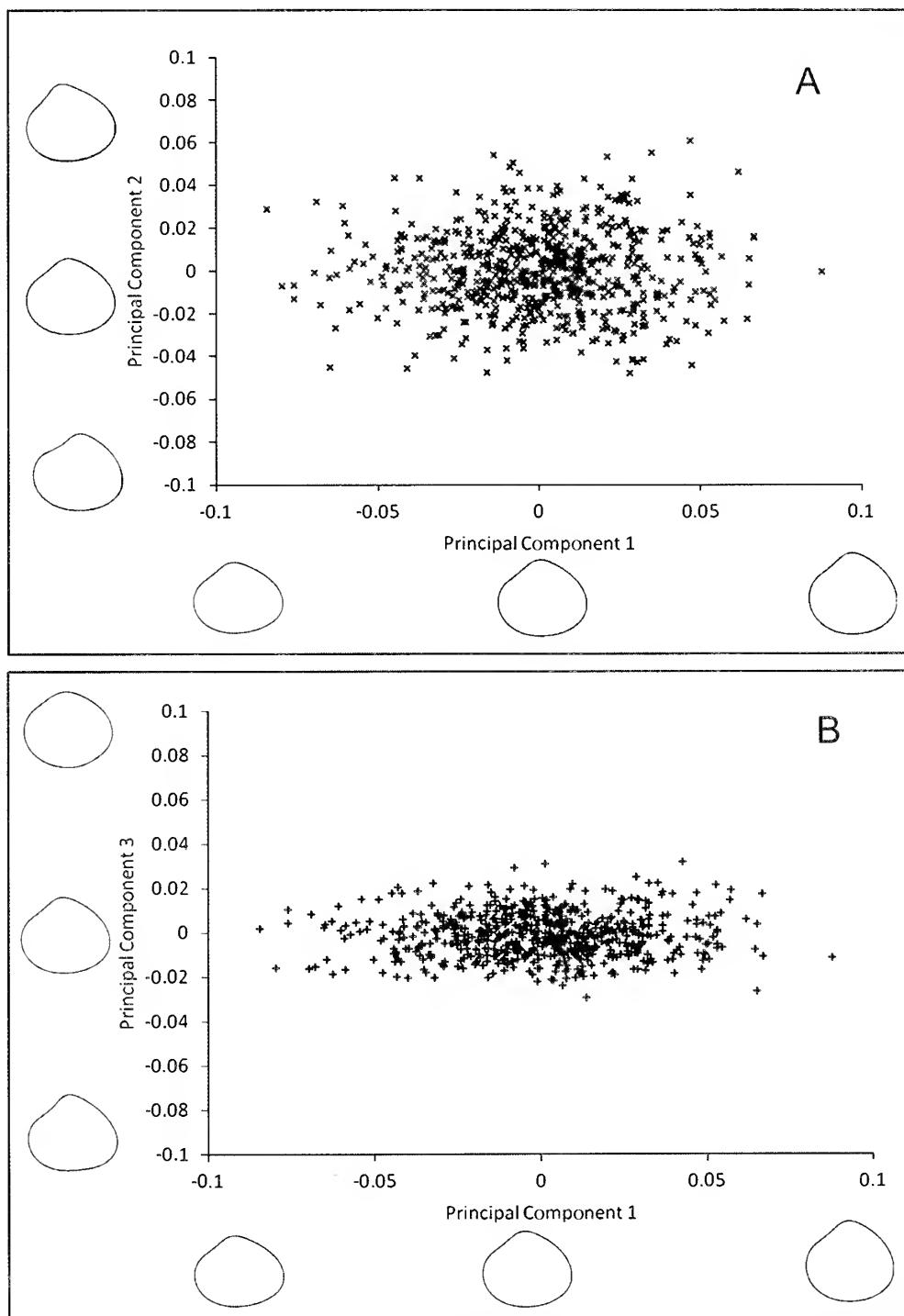
**Table 2.** Eigenvalues and contribution of principal components of *Astarte borealis* in this study.

Component	Eigenvalue	Proportion (%)	Cumulative (%)
PC 1	7.36E-04	47.4171	47.4171
PC 2	3.53E-04	22.7443	70.1614
PC 3	2.02E-04	13.0451	83.2065
PC 4	5.23E-05	3.3717	86.5782
PC 5	4.26E-05	2.7436	89.3218
PC 6	2.68E-05	1.7263	91.0482
PC 7	2.04E-05	1.3167	92.3649
PC 8	1.65E-05	1.0634	93.4282
PC 9	1.29E-05	0.8343	94.2625
PC 10	1.05E-05	0.6759	94.9384

the observed morphological variations. Table 2 has first 10 PC of the recent *A. borealis* outline analysis as computed by PrinComp. The 10 PCs account for about 94.94% of the variance found in the population, and the first three PCs represent 83.21% of variance.

The PCs were plotted against one another to show the concentration of variance in outline shapes (Figure 5). The greatest variation is represented by the first PC, the second greatest variation by the second PC and so forth. The distribution of variation can be visualized by plotting the PCs against one another, since the first two PCs comprise the most variation; they are plotted with the PC 1 on the x-axis and the PC 2 on the y-axis. Figure 5 shows the first and second principal components plotted with the outline contours drawn by the PrinPrint program, as well as the first and third principal components. As shown on Figure 5, PC 1 accounts for 47.42% of the variance found in the recent specimens and based on the visualization this is representative of relative shell height. From the positive to the negative standard deviations, the shell length only varies about 1% whereas the shell height varies about 15%. The positive standard deviation has a height to length ratio of 1.09, the mean shape ratio is 1.17 and the negative standard deviation has a ratio of 1.26. The mean ratio of 1.17 is consistent with the bivariate analysis results of length to height ratios (Table 1). PC 2 accounts for 22.74 % of the variance and represents the position of the umbones with respect to the central line. The mean shape has an umbo nearly on the midline, the positive deviation has the umbo quite dorsal to the midline and the negative deviation has the umbo slightly dorsal of the midline. PC 3 accounts for 13.05 % of the variance and is representative of the overall shell shape. The positive deviation has a rounded, subquadrate figure ranging to the negative valve with a compressed subtrigonal shape. This is consistent with the various descriptions available in literature. No correlations occurred when PC 2 and PC 3 were plotted against one another.

The shell outline was analyzed for 11 fossil specimens and results were plotted over the recent graphs for comparison (Figure 6). Fossil specimens fall entirely within the range of the recent specimens data. Since sample size is different, 641 recent samples and 11 Pliocene

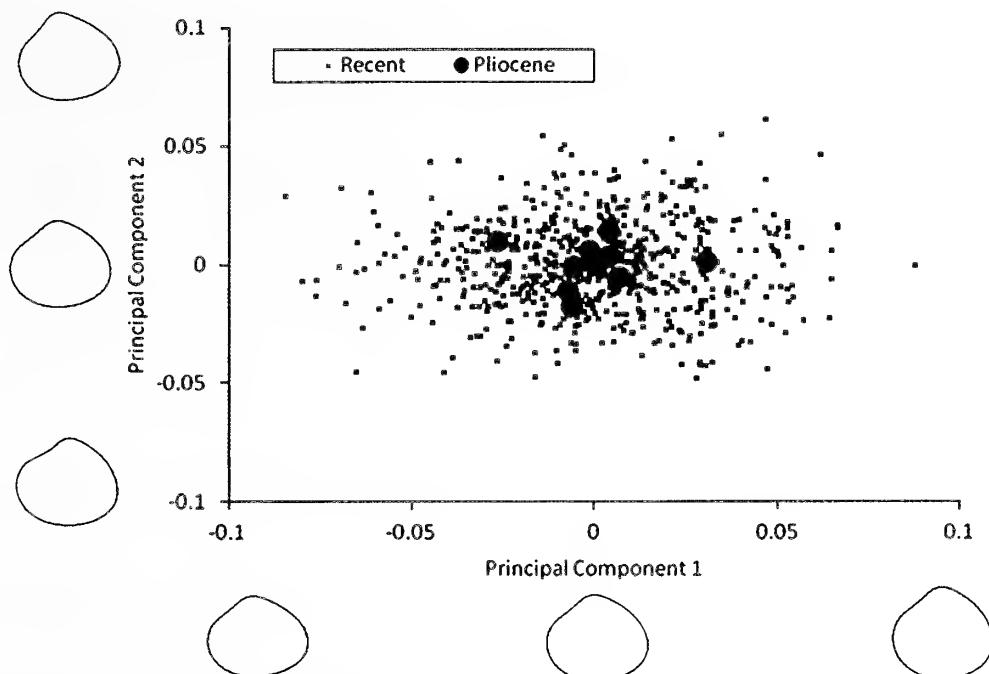


**Figure 5.** Plots of principle components. A. PC 1 vs. PC 2 of *Astarte borealis* with reconstructed contours. B. PC 1 vs. PC 3 of *A. borealis* with reconstructed contours.

fossil samples, one-way Kruskal and Wallis ANOVA was used to test the significant of differences ( $p < 0.0001$ ) between the recent and fossil *A. borealis* PC 1 results (Kruskal and Wallis, 1952). This is interpreted as an indication that the morphological variability of fossils is similar to that of the recent specimens, however not a direct indicator of correspondence.

Existing paleontological descriptions of fossil and recent species of *Astarte* suggest great similarity in shape among species. Use of elliptical Fourier analysis is an attempt to show that the outline of fossil clams match the modern and fall into the same distribution.

Morphologic variability of shell is one of the main criteria used for identification of fossil species of bivalve



**Figure 6.** Principal Component 1 vs. Principal Component 2 for recent and Pliocene *A. borealis*.

mollusks. It is, therefore, important to understand the limits of morphologic variability within the same species and population of bivalve mollusks, particularly the ones lacking prominent and diagnostic morphologic characteristics.

Outline shape analysis clearly indicates that *Astarte borealis* has a high morphological variability at the species level and even within a single population, which can be a potential source of confusion during species identification, especially with the use of qualitative descriptive parameters for shell shape. The bivariate comparison analysis between Pliocene and recent populations shows that there is continuity in the species and that the variation has been a characteristic of the species for a long time. The multivariate outline analysis indicates that the intraspecific variation is based upon a common shape that grades into other shapes evenly or a correlated population centered on a common "central" form. This study does not support the idea that the variation within certain species is a continuum between two end forms. For the studied population of *Astarte borealis*, allocation to forms and varieties would be at best problematic. Separation of fossil species in the absence of a large specimens sample should not be based solely on the shell outline and should include other diagnostic characteristics, such as external sculpture, details of the hinge, and features of the shell margin.

The study of geographical distribution of species by Zettler (2002) emphasized and confirms the polymorphism of *A. borealis*. The polymorphism of the species has been attributed to non-pelagic reproduction that causes the eggs to attach to the substrate near the parents (Bernard, 1979; Ockelman, 1958). Since there is a lack of diversity in reproduction due to limited genetic

mixing and a greater chance of isolation in the population, the variation could accelerate depending upon environmental conditions such as substrate composition, salinity, temperature, and nutrients. The slight differences in environment may influence the changes in the shell height to length ratio or perhaps the ventral margin that affect a certain portion of the population but do not separate it from the species. Changes can probably be detected in shell thickness and overall size, which could be a function of water temperature. That, in turn would be a function of changing climate.

#### ACKNOWLEDGMENTS

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# Reviving a cold case: two northeastern Pacific dendrodorid nudibranchs reassessed (Gastropoda: Opisthobranchia)

Jeffrey H.R. Goddard

Marine Science Institute  
University of California  
Santa Barbara, CA 93106-6150 USA  
goddard@lifesci.ucsb.edu

Ángel Valdés

Department of Biological Sciences  
California State Polytechnic University  
3801 West Temple Avenue  
Pomona, CA 91768-4032 USA  
aavaldes@cpp.edu

## ABSTRACT

Ten nominal species of dendrodorid nudibranchs are known from the NE Pacific Ocean, including the Gulf of California. However, disagreement surrounds the taxonomic status of *Doriopsilla nigromaculata* (Cockerell in Cockerell and Eliot, 1905) and *Doriopsilla rowena* Marcus and Marcus, 1967, including the correct generic placement of the former. To resolve this disagreement, we examined type specimens, the original descriptions, and unpublished materials in the James Lance Collection at the California Academy of Sciences and conclude that *Doriopsilla nigromaculata* is: (1) a member of *Dendrodoris*; (2) not synonymous with the valid species *Doriopsilla rowena*; and (3) a senior synonym of *Dendrodoris behrensi* Millen and Bertsch, 2005. Like other members of the genus, *Dendrodoris nigromaculata* has a centered anus, smooth dorsum, delicate wavy mantle edge, and possesses both ptyaline and esophageal glands. It is translucent white with chocolate brown blotches, the larger of which are usually clustered into three or four groups centered mid-dorsally. In contrast, *Doriopsilla rowena* has an off-center anus, a papillate and densely spiculate dorsum with a stiff margin, and lacks both ptyaline and esophageal glands. Its scattered brown flecks and larger, round concentrations of opaque white distinguish it dorsally, and notal spicules include rods and forks. *Doriopsilla rowena* grows to 12 mm long and has been found in La Jolla, California, the Pacific coast of Baja California, and the northern Gulf of California south to Panama. *Dendrodoris nigromaculata* grows to 27 mm and is known from Monterey, California south to the San Benitos Islands, Baja California. Both species have large eggs and metamorphic direct development, but small eggs indicating planktotrophic development have also been observed in *D. rowena* from Jalisco, Mexico, suggesting *D. rowena* may constitute a cryptic species complex or display poecilogeny.

*Additional Keywords:* Dendrodorididae, Nudibranchia, nomenclature

ing the Gulf of California (Behrens and Hermosillo, 2005); *Dendrodoris azineae* Behrens and Valdés, 2004; *Dendrodoris behrensi* Millen and Bertsch, 2005; *Dendrodoris fumata* (Rüppell and Leuchart, 1831); *Dendrodoris stohleri* Millen and Bertsch, 2005; *Doriopsilla albopunctata* (Cooper, 1863); *Doriopsilla gemela* Gosliner, Schaefer and Millen, 1999; *Doriopsilla janaina* Marcus and Marcus, 1967; *Doriopsilla nigromaculata* (Cockerell in Cockerell and Eliot, 1905); *Doriopsilla rowena* Marcus and Marcus, 1967; and *Doriopsilla spaldingi* Valdés and Behrens, 1998. However, an important taxonomic disagreement remains in the modern literature. Camacho-García et al. (2005) considered *Doriopsilla rowena* a valid species, whereas Behrens and Hermosillo (2005) regarded it as a junior synonym of *Doriopsilla nigromaculata*. The suggested synonymy of *D. nigromaculata* and *D. rowena* was raised as a possibility by James Lance in Keen (1971: 830; cited as *Doriopsilla nigromaculata*) and again by McDonald (1983: 171; cited as *Dendrodoris nigromaculata*). However, if Camacho-García et al. (2005) were correct, and *Doriopsilla rowena* is valid, then *D. nigromaculata*, which was originally described based on a single specimen collected by Cockerell in La Jolla, California, has either remained unknown since its original description and should be regarded as a *nomen dubium*, or has since been described under another name.

A contributing factor to this disagreement is that historically the distinctions between *Dendrodoris* and *Doriopsilla* have been confusing, including for species from the northeast Pacific Ocean (reviewed by Steinberg 1961; Valdés and Ortea 1997; Gosliner et al. 1999). However, Valdés et al. (1996) and Valdés and Ortea (1997) provided clear anatomical and morphological criteria separating the two genera, and recent phylogenetic analyses support this separation (Valdés and Gosliner 1999, Valdés 2003). Here, we use these criteria and the examination of type specimens to first establish the correct generic placement of *D. rowena* and *D. nigromaculata*, ruling out the synonymy of these two species. Then we compare their original descriptions with those of other species of dendrodoridids known from the region to

## INTRODUCTION

Ten nominal species of dendrodorid nudibranchs are currently recognized from the NE Pacific Ocean, includ-

show that (1) *Doriopsilla rowena* is valid, and (2) that one species described recently from the region is in fact a junior synonym of *Dendrodoris nigromaculata*. In both steps we also draw from extensive materials in the James R. Lance Collection at the California Academy of Sciences in San Francisco (hereafter, Lance Collection). These constitute new evidence not available prior to Lance's death in 2006 and shed light on what had effectively become a taxonomic cold case.

## MATERIALS AND METHODS

To establish the generic placement of *Doriopsilla nigromaculata* and *Doriopsilla rowena*, we extracted from their original descriptions information on four morphological and two anatomical characters which taken together can be used to separate *Dendrodoris* from *Doriopsilla* (Table 1). We corroborated this information by examining the type specimens of both species, which were obtained, respectively, from The Natural History Museum, London (NHMUK) and the U.S. National Museum of Natural History (USNMH). We also examined Lance's specimens of *D. rowena* in the Invertebrate Zoology and Geology collection at the California Academy of Sciences (CASIZ) and used his description of *D. rowena* in Keen (1971), as well as his unpublished notes, 35mm photographic slides, and illustrations in the Lance Collection. Lance kept many of these materials organized by species in folders, which contain information on the morphology, color, anatomy, egg masses, and development of living specimens of most of the dendrodoridids known from the northeast Pacific Ocean. The folder for *D. rowena* in particular supplements Mareus and Marcus's original (1967) description of *D. rowena*, which was based on preserved material. Where appropriate, we refer to species folders in the Lance Collection by their names; field accounts by number, date, and locality; and 35mm slides by date and locality when possible. To compare *D. nigromaculata* with other species of *Dendrodoris* from the northeast Pacific Ocean, we used information from our examination of the type specimen, as well as from the Lance Collection, Behrens and Hermosillo (2005), Millen and Bertsch (2005), and Goddard (2005). Finally, we used the online searchable database of the California Academy of Sciences Invertebrate Zoology collection ([http://research.calacademy.org/redirect?url=http://researcharchive.calacademy.org/research/izg/iz\\_coll\\_db/index.asp](http://research.calacademy.org/redirect?url=http://researcharchive.calacademy.org/research/izg/iz_coll_db/index.asp)) to obtain additional and otherwise unpublished locality information to further document the known geographic distribution of these species. Here, we used information for specimens identified by established authorities familiar with the nudibranch fauna of the region. These are referenced below by CASIZ and the corresponding catalog numbers.

## RESULTS

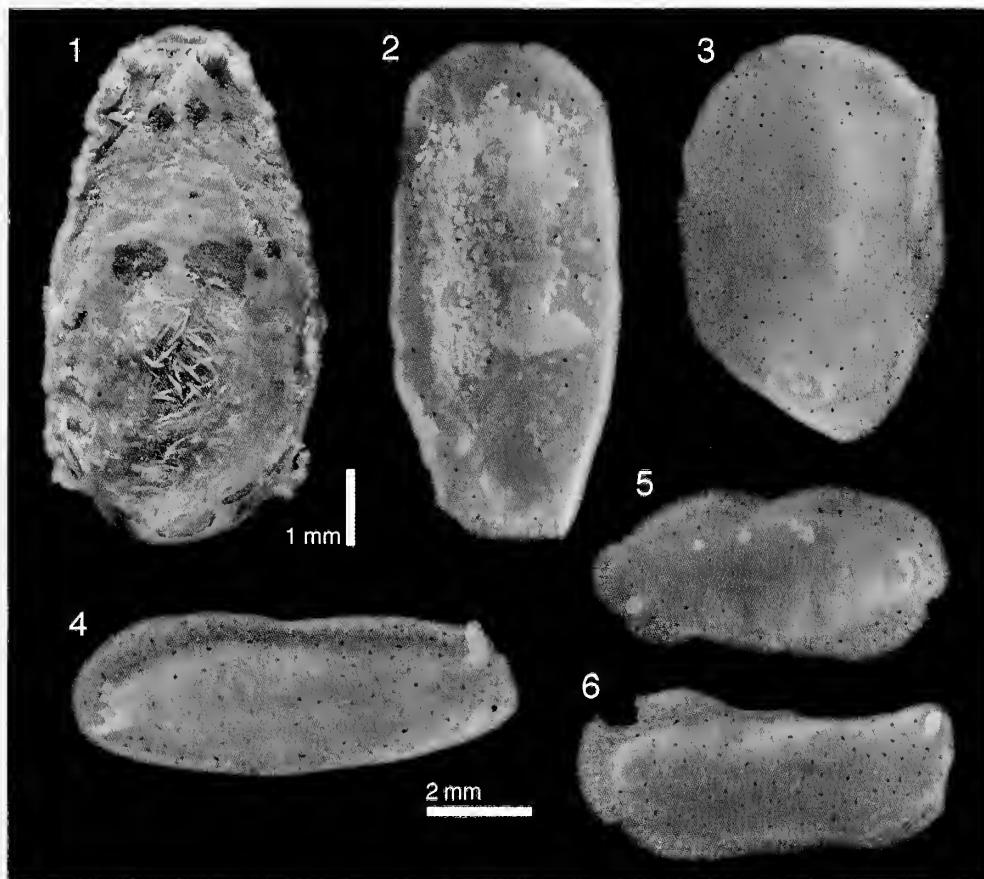
### DESCRIPTION OF RELEVANT MATERIALS IN THE LANCE COLLECTION

**1. Species Folder:** *Doriopsilla rowena* contains: (1) A hand-written description, accompanied by pencil sketches, of this species with the manuscript name "Doriopsilla puertecitensis" (later, Lance wrote the name *D. rowena* in red ink on this description). The pencil sketches are based on living specimens (CASIZ 182606) collected 20 March 1965 from 4.4 mi south of Puertecito, Baja California, and include dorsal and ventral views of an adult, details of the notum and notal spicules, and penis. The description also includes a sketch and brief description of an egg mass laid by a 12 mm adult. (2) Six separate pen and ink illustrations, all labeled as *Doriopsilla rowena* and clearly based on the above pencil sketches. (3) A sheet labeled "Doriopsilla rowena – Field Account Data" for sites in the Gulf of California. The dates listed include years from 1954 to 1979, and out of 10 sites listed record *D. rowena* only from Puerto Peñasco. (4) One clear plastic sheet holding 35 mm slides from 1966 and 1969, the earliest labeled first as "Dendrodoris sp." and later as "Doriopsilla rowena or *D. nigromaculata*?"

**2. Species Folder:** *Doriopsilla nigromaculata* contains: (1) A list of specimens found at South Casa Reef and Windansea Reef, both in La Jolla, California. (2) A lined sheet with dorsal and ventral sketches of an adult from La Jolla. The notation "F.A. 181" on this sheet refers to Field Account 181, which was for 25 June 1967 at South Casa Reef, La Jolla. This sheet is first labelled as "Brown spotted *Doriopsilla*," with "? *D. nigromaculata*" later added in red ink. (3) A note stating "*D. nigromaculata* Published sketch in Opis. News. 14(8): 29 of hatching." (4) A three page typed description of this species with the

**Table 1.** Select diagnostic characters distinguishing *Dendrodoris* from *Doriopsilla*. Based on Valdés et al. (1996) and Valdés and Ortea (1997).

Character	<i>Dendrodoris</i>	<i>Doriopsilla</i>
Mantle	Smooth and soft, rarely with large tubercles	Hard and tuberculate
Mantle spicules	Absent or isolated	Strong network, including in tubercles
Mantle margin	Delicate, wavy	Stiff
Position of anus relative to midline of body	Centered	Off-center
Ptyaline glands	Present	Absent
Esophageal glands	Present	Absent



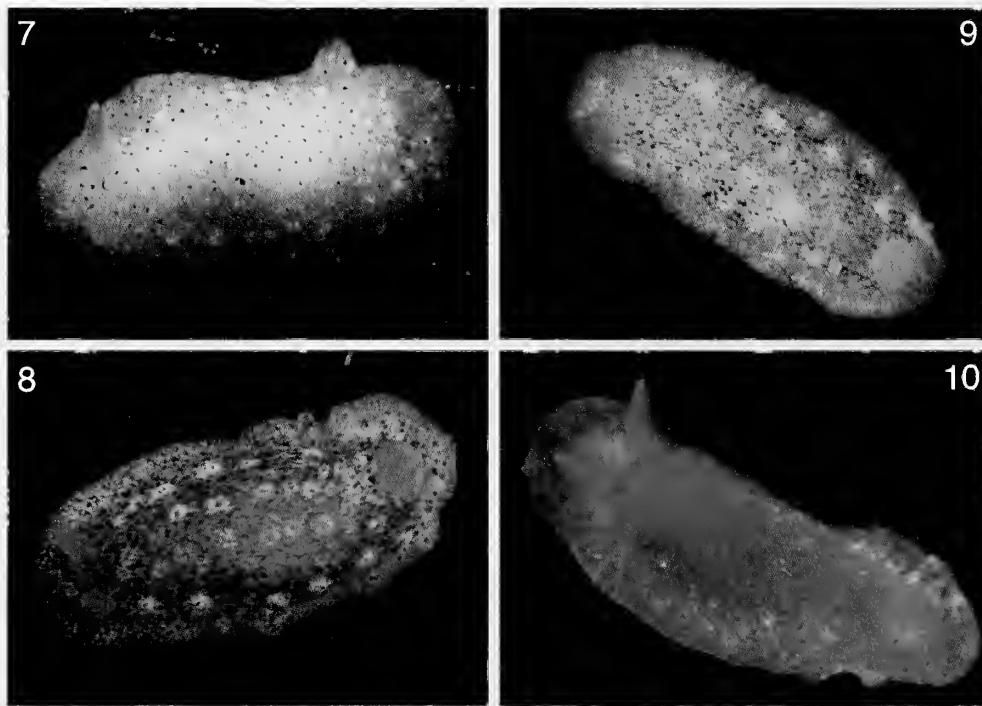
**Figures 1–6.** Type specimens. **1.** *Dendrodoris nigromaculata* (NHMUK 1904.7.7.1). Photo by Harry Taylor. **2–6.** *Doriopsilla rowena* (USMNH 678413). Photos by Chris Meyer.

heading “*Doriopsilla nigromaculata* (Cockerell and Eliot, 1905) Figs. 1–7.” The figures for this description and legend are on a separate sheet and are a composite of copies of the six pen and ink illustrations from the Species Folder for *Doriopsilla rowena*, plus a map of California with a single red ink dot showing “Distribution in California.” The description is based on the four specimens Lance found in La Jolla on 25 June 1967 but refers to the specimen from La Jolla described by Cockerell and Eliot 70 years earlier. (5) Two sheets with sketches and notes on egg masses laid by specimens collected at Windansea Reef in 1968, San Quintín in 2001, and South Casa Reef in 1998. (6) Two sheets containing 35 mm photographic slides, one with images of adult specimens, the other with images of egg masses and hatching juveniles.

**3. Species Folder: White Porostome Spotted** contains: (1) A sheet titled “Crenulate dorid” with sketches in pencil of two specimens and a brief description, including dimensions of 24 × 5 mm and 27 × 5 mm. This sheet is undated but the dimensions of the larger specimen, combined with information in (2) below indicate that these specimens were collected in either 1961 from the Coronados Islands or in 1963 from Point Loma,

San Diego. (2) A hand-written description of this species with the manuscript name “*Dendrodoris barbarensis*,” based on a single specimen collected from 8 m depth at Naples Reef, Santa Barbara County 30 Oct 1966, two specimens collected at 30 m depth 1.6 km south of South Coronado Island by Nan Limbaugh on 22 Apr 1961, and two specimens collected intertidally at Point Loma by Wesley Farmer on 29 Oct 1963. (3) A typed sheet with information on three specimens collected intertidally at Lunada Bay, Palos Verdes Peninsula, by William Jaeckle, 20 Apr 1983. A note indicates that one of these specimens laid an egg mass on 4 May 1983. (4) Pencil notes and sketches of an egg mass laid by an individual collected from South Casa Reef, La Jolla, 20 July 1974, and sketches of the subsequent direct development to hatching juveniles from that egg mass.

**4. Field Account 181** (June 25, 1967, South Casa Reef, La Jolla) contains, in addition to the annotated list of opisthobranchs found on that date by Lance (and Barbara Good), contains notes, from three separate dates, on the development of embryos in an egg mass deposited by *Doriopsilla rowena* (cited as “doriopsillids,” with a later notation as “*Doriopsilla nigromaculata*?”) collected on that date.



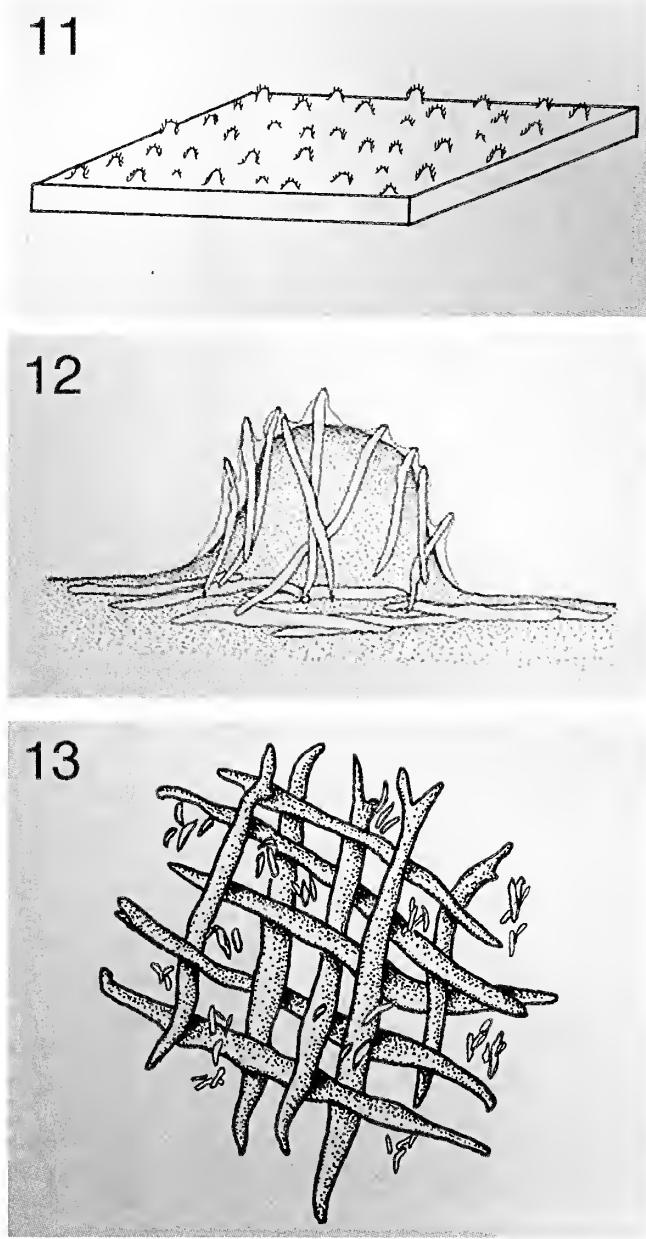
**Figures 7–10.** Living adult *Doriopsilla rowena*. **7.** Percebu, Gulf of California, Baja California, 7 April 1966 (35 mm slide in Lance Collection, Species Folder: *Doriopsilla rowena*). **8.** Total length 9.2 mm, San Quintin, Baja California, 16 November 2001 (35 mm slide in Lance Collection, Species Folder: *Doriopsilla nigromaculata*). **9.** South Casa Reef, La Jolla, California, 25 June 1967 (35 mm slide in Lance Collection, Folder: *Doriopsilla nigromaculata*). **10.** Total length (in  $\text{MgCl}_2$ ) 6.7 mm, Lindo Mar, Bahía de Banderas, Jalisco, Mexico, 26 Feb. 2006 (CASIZ 174055; Goddard and Hermosillo, 2008, as *Doriopsilla nigromaculata*).

#### GENUS-LEVEL TAXONOMY

***Doriopsilla nigromaculata*.** In the original description of *D. nigromaculata* Cockerell and Eliot (1905) described the mantle of a single preserved specimen as “smooth, not tuberculate,” with a “rather narrow” margin. The latter is consistent with the delicate margin characteristic of living specimens of *Dendrodoris* (Table 1) and is visible in the type specimen (NHMUK 1904.7.7.1) as upturned, crenulate and soft in appearance (Figure 1). Cockerell and Eliot (1905) mentioned “a number of glistening white spicules...imbedded in the skin” of the mantle and described them as “mostly fairly straight long rods, but some of the smaller ones are bent and have an irregular outline.” The spicules are not described as being regularly or densely arrayed and are visible in the type specimen where the mantle tissue had been carefully scraped away, presumably by Eliot in his original examination of the specimen (Figure 1). The position of the anus can be inferred as centered based on their description of the gill plume as “set in a semicircle open behind.” Internally, they described a “folliculate” mouth gland “with a fairly long duct,” which is clearly a ptyaline gland (e.g., illustrations in Valdés et al., 1996; Millen and Bertsch, 2005). No esophageal glands were mentioned, but these are minute (Valdés et al. 1996; Millen and Bertsch, 2005, Figure 2) and likely would not have garnered attention. All of these traits, as well as the extreme anterior and posterior position of the rhinophores and

gills, respectively, in the type specimen, are consistent with contemporary descriptions of species of *Dendrodoris* and clearly indicate the correct generic of *D. nigromaculata* is *Dendrodoris* (Table 1).

***Doriopsilla rowena*.** Marcus and Marcus (1967) described *D. rowena* based on seven preserved syntypes, five of which remain (USNMH 678413), and notes by the collector on the color of the living animals, which were collected in Puerto Peñasco, Sonora, Mexico, in the northern Gulf of California (Figures 2–6). They described the mantle as “smooth,” with evidence of large, but dissolved, diagonally crossed spicules in the “connective tissue of the back.” They noted that “the thick anal papilla and the renal pore in front of it lie to the left of the branchial tuft,” clearly indicating the eccentric position of the anus. The anterior part of the alimentary tract is illustrated in their figure 62B, and does not show either ptyaline or esophageal glands. Elsewhere, Marcus and Marcus (1967: 99) state that the absence of a ptyaline gland is one characteristic of *Doriopsilla*. Marcus and Marcus (1967) did not describe any dorsal tubercles in *D. rowena*. However, James Lance, who found and observed living specimens of this species from Puertecitos, Baja California, and Puerto Peñasco, both in the northern Gulf of California (Figures 11–12), illustrated minute, spiculate dorsal tubercles, which was confirmed with examination of Lance’s original specimens (CASIZ 182606). Lance also illustrated the pattern and



**Figures 11-13.** *Doriopsilla rowena*, details of notum; all from Lance Collection, Species Folder: *Doriopsilla rowena*. **11.** 1×1 mm detail of notal surface. **12.** Notal tubercle with spicule detail. **13.** Notal spicule pattern.

shapes of the notal spicules (Figure 13), which consist of diagonally crossed rods and forks (Lance Collection, Species Folder: *Doriopsilla rowena*). Taken together, these traits indicate that *D. rowena* is indeed a *Doriopsilla*, as originally described by Marcus and Marcus (1967) (Table 1). This was further confirmed with the examination of the syntypes (Figures 2–6), which are relatively flat and wide animals covered with small spiculate tubercles and an eccentric anus. All these traits are consistent with the diagnosis of *Doriopsilla* by Valdés and Gosliner (1999).

#### SPECIES-LEVEL TAXONOMY

***Doriopsilla rowena*.** Based on the above morphological and anatomical differences, *Doriopsilla rowena* cannot be a synonym of *Dendrodoris nigromaculata*. *Doriopsilla rowena* differs externally from all other congeners known from the region in its small adult size (up to 12 mm total length) and unique color pattern, consisting of small reddish-brown flecks scattered over the dorsum, as well as larger, round concentrations of opaque white, frequently arranged in longitudinal series, against a ground color of off white to pale yellow, pink or orange (Marcus and Marcus, 1967; Lance in Keen 1971; Behrens and Hermosillo, 2005, cited as *Doriopsilla nigromaculata*; Camacho-García et al., 2005) (Figures 2–10). *Doriopsilla rowena* is therefore a valid species.

***Dendrodoris nigromaculata*.** Cockerell and Eliot (1905) based their original description of *D. nigromaculata* on a single specimen, 10 mm long preserved, that was collected in July 1901 from La Jolla, California (Figure 1). The color of the preserved specimen was described as “yellowish-drab with a slight inclination to lilac in places,” with “a double border of black spots round the dorsal margin, and a few larger black blotches symmetrically disposed, one in front of the rhinophores, two behind them, two in the middle of the back, and five in front of the branchiae.” These larger blotches are still visible in the type specimen (Figure 1). Two nominal species of *Dendrodoris* from the northeast Pacific Ocean have dark spots against a pale background: *D. behrensi* Millen and Bertsch, 2005 (Figure 17) and *D. stohleri* Millen and Bertsch, 2005. In *D. stohleri* the black spots are relatively uniform in size and scattered over the entire dorsum, save its margin (Millen and Bertsch, 2005). However, comparison of the color patterns originally described for *D. nigromaculata* and *D. behrensi* reveals a virtually identical match (Table 2). Indeed, the only discrepancy between the descriptions of these two species is that Millen and Bertsch (2005: 195) state that *D. behrensi* lacks mantle spicules. However, in the companion paper to Millen and Bertsch (2005), Goddard (2005) illustrated and described “slightly curved, spindle-shaped spicules” arranged in a lattice in *D. behrensi* recently hatched (Figure 21) from egg masses laid by adults (Figure 17) included as paratypes of *D. behrensi* by Millen and Bertsch (2005). Lance was also familiar with this species and observed egg masses and hatching juveniles virtually identical to those described by Goddard (2005) (Lance Collection, Species Folder: White Porostome Spotted) (Figures 18–20). Moreover, Lance described the adult body of this species as “very slightly spiculose with notal margins non spiculose” (Lance Collection, Species Folder: White Porostome Spotted). The density of notal spicules therefore decreases as juveniles grow into adults, which could make the spicules easily overlooked in living adult specimens. A similar phenomenon was recently documented by Sánchez-Tocino et al. (2014) for some chromodorid nudibranchs.

**Table 2.** Comparison of original descriptions of external color of a single preserved *Dendrodoris nigromaculata* and living *Dendrodoris behrensi* by Cockerell and Eliot (1905) and Millen and Bertsch (2005), respectively.

	<i>Dendrodoris nigromaculata</i> (Cockerell and Eliot, 1905)	<i>Dendrodoris behrensi</i> Millen and Bertsch, 2005
Background color	“yellowish-drab with a slight inclination to lilac in places”	“semi-translucent white or pale cream”
Larger spots	Black, “symmetrically disposed:”	Dark reddish brown or chocolate brown, “clustered in four areas in the mid line:”
Position		
Group 1	“in front of the rhinophores”	“in front of the rhinophores”
2	“behind [rhinophores]”	“behind the rhinophores”
3	“middle of back”	“middle of the body”
4	“in front of the branchiae”	“in front of the gills”
Smaller spots	“double border... round the dorsal margin”	“scattered towards the edges of the dorsum”
Other color elements	None	None

With no significant differences between their original descriptions, *Dendrodoris behrensi* is therefore a junior synonym of *Dendrodoris nigromaculata*.

## SYSTEMATICS

Based on the taxonomic results described above, a new systematic arrangement and list of synonyms is proposed for *D. rowena* and *D. nigromaculata*.

Family Dendrodorididae O'Donoghue, 1924

### Genus *Doriopsilla* Bergh, 1880

#### *Doriopsilla rowena* Marcus and Marcus, 1967 (Figures 2–16)

*Doriopsilla rowena* Marcus and Marcus, 1967: 205–207; Keen, 1971: 830; Poorman and Poorman, 1978: 373; Bertsch and Kerstitch, 1984: 267; Valdés and Ortea, 1997: 253; Gosliner et al., 1999: 209; Valdés and Gosliner, 1999: 338–340; Camacho-García et al., 2005: 80; Goddard and Hermosillo, 2008: 87; Angulo-Campillo, 2005: Table 2.

*Dendrodoris* (?) *nigromaculata* [non Cockerell in Cockerell and Eliot, 1905] – Behrens, 1980: 58.

*Dendrodoris nigromaculata* [non Cockerell in Cockerell and Eliot, 1905].—Steinberg 1961: 59; Sphon 1972: 61; McDonald and Nybakken, 1980: 52; Lance, 1982: 29; McDonald, 1983: 170–171; Behrens, 1991: 71; Angulo-Campillo, 2003: Table 2; Goddard, 2004: 1959, 1963; Goddard, 2005: 206.

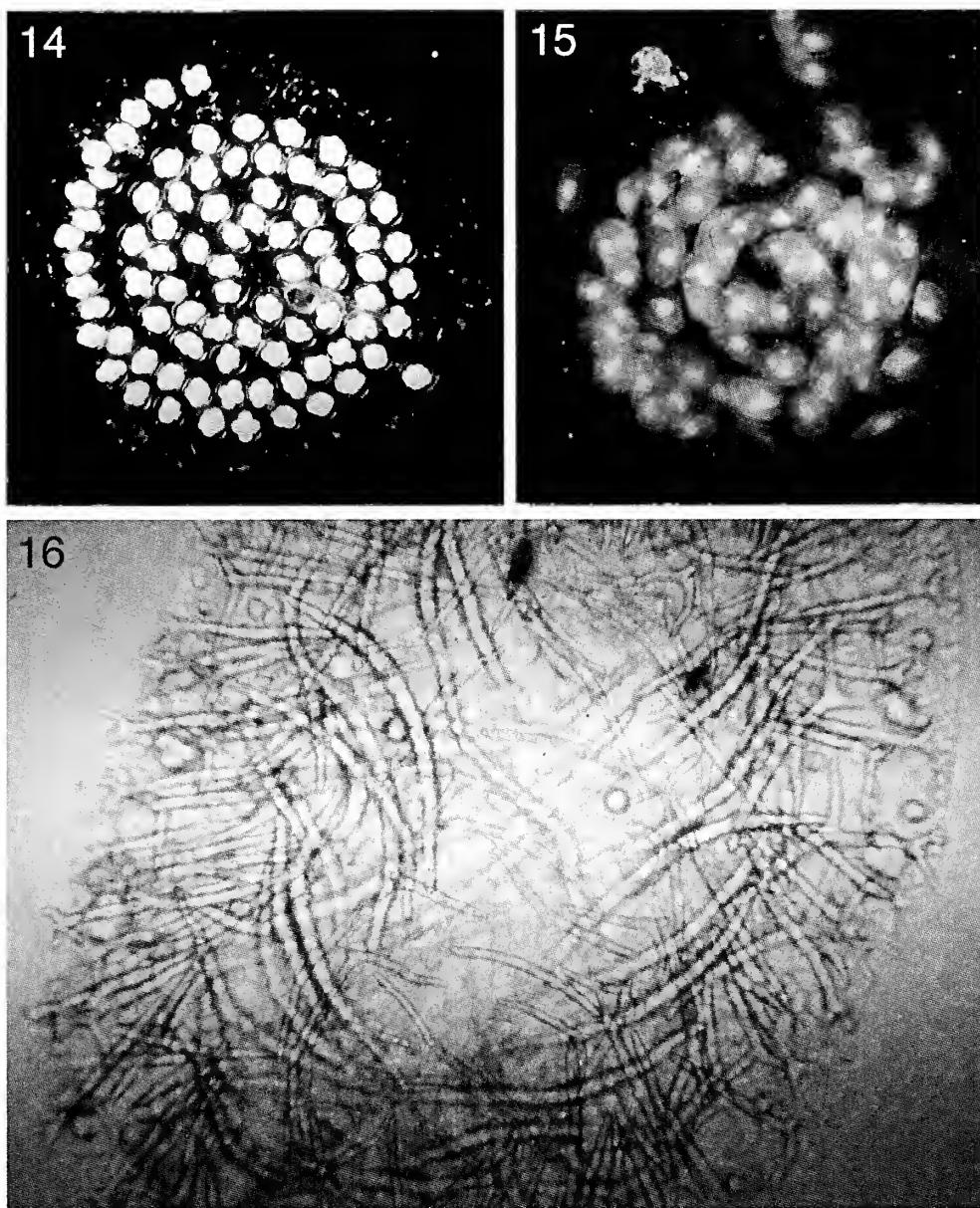
*Doriopsilla nigromaculata* [non Cockerell in Cockerell and Eliot, 1905].—Behrens and Hermosillo, 2005: 88; Lance Collection, Species Folder: *Doriopsilla nigromaculata*. California Academy of Sciences and Goddard, 2013: worksheets for Ladera St., False Point, Windansea, and So. Casa Reef (data from unpublished field accounts, no page numbers).

**Type Material:** *Doriopsilla rowena* – Syntypes: 5 specimens, Puerto Peñasco, Sonora, Mexico (USNMH 678413).

**Anatomy:** The anatomy of *D. rowena* was described by Marcus and Marcus (1967), with additional details presented by Valdés and Gosliner (1999). Further, as noted and illustrated by Lance, the notum is densely spiculate with rods and forks (Figures 12–13, 16).

**External Morphology:** The external morphology of *D. rowena* was described by Marcus and Marcus (1967), with additional details presented by Lance (Lance Collection, Species Folders: *Doriopsilla rowena* and *Doriopsilla nigromaculata*) and Lance in Keen (1971). Living adults reach 12 mm in length. The dorsum is flecked with dark brown, has larger, round concentrations of opaque white, typically in longitudinal series, and is covered by minute, spiculate tubercles (Figures 7–12). The ground color varies from whitish to yellow to pinkish orange.

**Development:** Lance obtained egg masses and observed development of *Doriopsilla rowena* from La Jolla (Figures 14–16). The egg ribbons were tightly coiled and laid flat, rather than on edge like most other dorid nudibranchs, and contained large eggs, encapsulated singly, that developed into hatching juveniles (Figure 15) in more than 26, but less than 38 days, at an ambient temperature of approximately 20° C (Lance Collection, Species Folder: *Doriopsilla nigromaculata*; Field Account 181, South Casa Reef, 25 June 1967). Recently hatched juveniles possess the same notal spicule complement of rods and forks as adults (Figures 13 and 16). Lance sketched another egg mass, laid by a specimen 9.5 mm long collected from Windansea Reef in June 1968. This egg mass was also laid flat and had 4 whorls in a closed spiral and a total diameter of 5 mm, as indicated by a scale bar. Based on that scale bar, the eggs illustrated by Lance measured approximately 215 µm in diameter. A note on Lance Field Account 181 indicates that the embryos did not develop a shell. Taken together, this information indicates that *D. rowena* from La Jolla have ametamorphic direct development (Bonar 1978; Goddard 2004). Lance's sketch and notes on an egg mass laid by a *D. rowena* from San Quintin, Baja California are also consistent with this mode of development.



**Figures 14–16.** *Doriopsilla rowena*, egg mass and hatching juveniles; all from 35 mm slides in Lance Collection, Species Folder: *Doriopsilla nigromaculata*. **14.** Egg mass from South Casa Reef, 26 Apr. 1998. **15.** Hatching juveniles, no date or locality (35 mm slide processed Sep. 1974). **16.** Spicule detail, hatched juvenile, South Casa Reef, no date (35 mm slide processed Sep. 1974).

(Lance Collection, Species Folder: *Doriopsilla nigromaculata*).

A specimen of *D. rowena* (Figure 10; CASIZ 174055), 6.7 mm long, collected from Nayarit, Mexico laid a flat egg ribbon of 6 turns in a closed spiral 6 mm across, virtually identical to the egg masses described above from La Jolla (JG, unpublished data). However, the eggs from Nayarit averaged 97.4  $\mu\text{m}$  in diameter, indicating planktotrophic development (Goddard and Hermosillo, 2008). Lance described similar egg masses laid by specimens of *D. rowena* from the northern Gulf of California but mode of development cannot be inferred based on any of the information included (Lance Collection, Species Folder: *Doriopsilla rowena*).

**Geographic Distribution:** *Doriopsilla rowena* is known from the northern Gulf of California to Panama, (Marcus and Marcus 1967; Keen 1971; Poorman and Poorman 1978; Bertsch and Kerstitch 1984; Camacho-García et al. 2005; Goddard and Hermosillo 2008; Angulo-Campillo 2005; CASIZ 171209, 171229), the Galapagos Islands (CASIZ 78390, 78408), and La Jolla, California to El Campo, near Punta Eugenia, Baja California Sur (Lance Collection, Species Folder: *Doriopsilla nigromaculata*; CASIZ 71519; Behrens and Hermosillo 2005) (Figure 22).

**Remarks:** As evidenced in the Lance Collection (Species Folder: *Doriopsilla rowena*), Jim Lance started to

describe *D. rowena* under the manuscript name “*D. puertecitensis*,” based on three specimens he collected at Puertecitos, on the Baja California side of the northern Gulf of California. Sometime following the publication of Marcus and Marcus (1967), Lance added in red ink the name *D. rowena* on his original pencil sketches of these specimens. Later he executed a set of undated pen and ink illustrations, some of which are reproduced here in Figures 11–13 and labeled them all as *Doriopsilla rowena* (these illustrations were likely made for the monograph on Panamic opisthobranchs that Lance intended but never completed). In the drawing of the dorsal view of an adult (not reproduced here) Lance depicted six thin, widely spread, bipinnate gills and a centered anus. However, examination of his original specimens from Puertecitos (CASIZ 182606) reveal more tightly clustered gills and an eccentric anus, indicating that Lance’s drawing in these respects was purely schematic.

On 25 June 1967 at South Casa Reef in La Jolla, Lance found four specimens of a small (up to 9 mm long) “doriopsillid” that he first referred to in his notes and illustrations as the “Brown-spotted *Doriopsilla*” but later changed in red ink to “?*D. nigromaculata*” (Lance Collection, Field Account 181 and Species Folder: *Doriopsilla nigromaculata*). He eventually found this species at three more sites on the outer coast of San Diego County, as well as in Bahía San Quintín, Baja California, and in his field accounts for these sites consistently used the name *Doriopsilla nigromaculata* for this species (Lance Collection; California Academy of Sciences and Goddard 2013).

Lance’s Species Folder for *Doriopsilla nigromaculata* includes a typed description, titled *Doriopsilla nigromaculata* (Cockerell and Eliot, 1905), which was based on the four specimens from La Jolla, California in June 1967. This description is accompanied by and references a composite figure, also labeled as *Doriopsilla nigromaculata*, but which was comprised solely of his earlier illustrations (eventually labelled as *D. rowena*) of “*D. puertecitensis*” from the Gulf of California (some of which are reproduced here in Figures 11–13). In the text of this description Lance states “it is likely that the present species and an unnamed one, frequently encountered in the Gulf of California, will eventually prove to be conspecific.” This indicates that Lance wrote this description after June 1967, but prior to receiving a copy of Marcus and Marcus (1967), and also suggests that after receiving the latter, he considered *D. rowena* a junior synonym of *D. nigromaculata*. Further, as mentioned above, hatching juveniles from La Jolla possess the same notal spicule complement of rods and forks as adults from the Gulf of California (Figures 13 and 16). Although morphologically the specimens from La Jolla are very similar to *D. rowena* from the Gulf of California, Lance never applied the name *D. nigromaculata* to the latter, and in conversation with at least one colleague, maintained that the two were probably distinct (T.M. Gosliner, personal communication to JG, 12 Dec 2014).

Lance (1982) illustrated a hatching juvenile, labeled as “*Dendrodoris nigromaculata* (Cockerell in Cockerell and

Eliot, 1905)”, the name used by California workers during this time period for what we have shown here to be *Doriopsilla rowena*. Lance noted publication of this illustration on a separate sheet in his Species Folder “*Doriopsilla nigromaculata*”. However, comparison of this illustration with his sketches of direct development in his species folder “White Porostome Spotted” reveals it to be copied from a sketch for that species, which we demonstrate here to be *Dendrodoris nigromaculata*. Although their egg masses and spicule complement as hatching juveniles are different, both species have ametamorphic direct development (see below), and Lance (1982) was probably mainly making a statement about developmental mode in the one. The unexpected twist is that the binomial used in the figure caption turns out to be accurate for the species actually illustrated.

The specimens described and identified as *D. rowena* by Bertsch and Aguilar-Rosas (1984) from El Tomatal, on the Pacific coast of Baja California, are, based on their larger size (up to 30 mm long) and color pattern, actually *Diaulula aurila* Marcus and Marcus (1967), which is common in that region (Bertsch et al. 1999, cited as “*Sal y pimenta*” (Salt and pepper [dorid]); Goddard and Schickel 2000, cited as *Discodoris* sp. 1 of Behrens 1991; personal observations).

### Genus *Dendrodoris* Ehrenberg, 1831

***Dendrodoris nigromaculata* (Cockerell in Cockerell and Eliot, 1905)**  
(Figures 1, 17–21)

*Doridopsis vidua* (?) [non Bergh, 1878].—Cockerell and Eliot, 1905: 40–41.

*Doris nigromaculata* Cockerell in Cockerell and Eliot, 1905: 40–41.

*Doridopsis nigromaculata* (Cockerell in Cockerell and Eliot, 1905).—Cockerell, 1908: 106.

*Dendrodoris vidua* [non Bergh, 1878].—O’Donoghue, 1926: 212.

*Dendrodoris nigromaculata* (Cockerell in Cockerell and Eliot, 1905).—O’Donoghue, 1926: 213; Steinberg, 1961: 59. Lance, 1982: 29.

*Dendrodoris* sp. Lee and Brophy, 1969: 20.

*Dendrodoris* sp. Behrens, 1980: 100; Behrens and Gatewood, 1986: 139, 142.

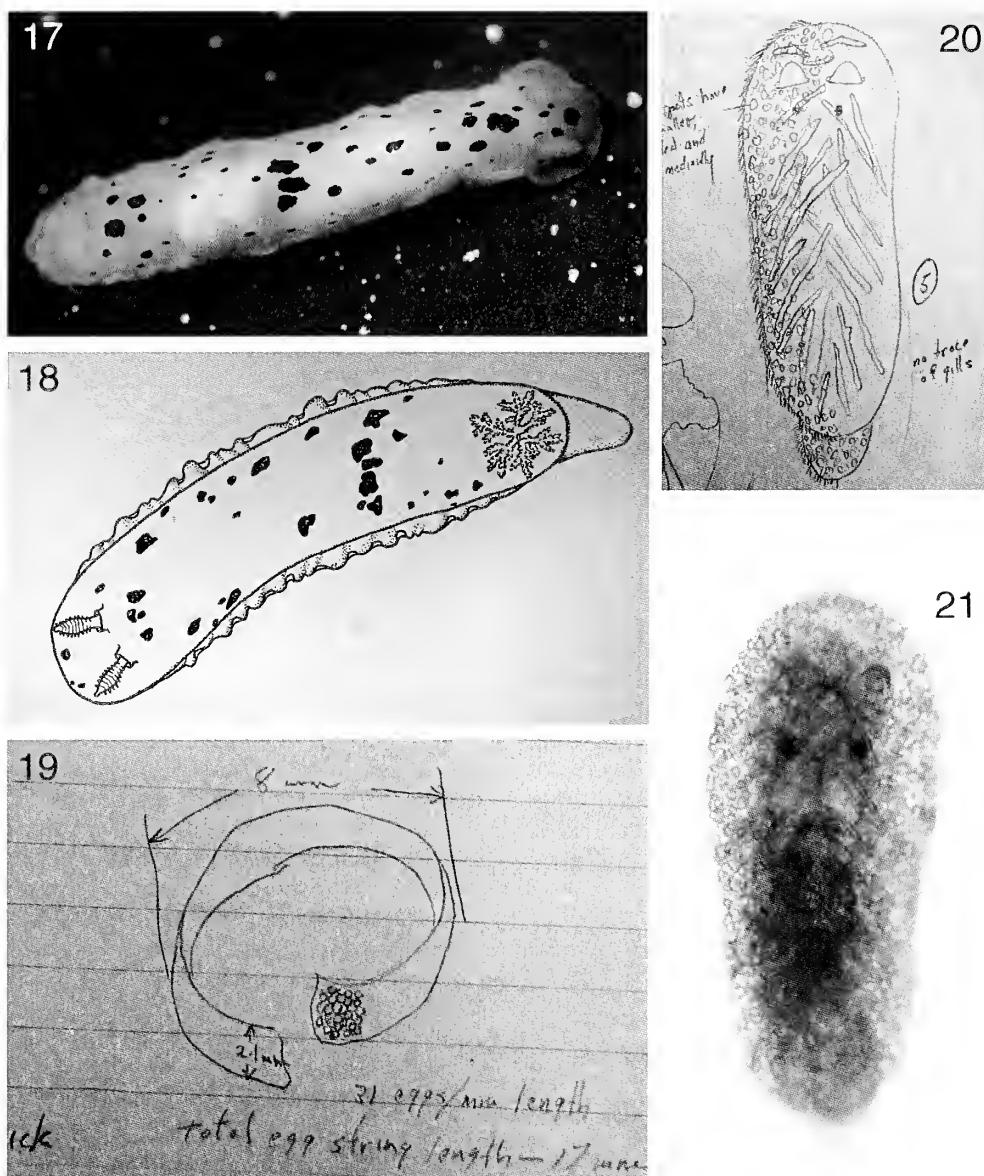
*Dendrodoris* sp. b McDonald and Nybakken, 1980: 54; McDonald, 1983: 171.

*Dendrodoris* sp. 3 Behrens, 1991: 72; Goddard, 2004: 1957, 1959, 1963.

*Dendrodoris behrensi* Millen and Bertsch, 2005: 189–199; Goddard, 2005: 201–211; Behrens and Hermosillo, 2005: 86; California Academy of Sciences and Goddard, 2013: worksheets for Hill St. and So. Casa Reef.

### Type Material:

*Doris nigromaculata* — Holotype: La Jolla, California, July 1901 (NHMUK 1904.7.7.1), dissected by Sir C. Eliot in 1905.



**Figures 17–21.** *Dendrodoris nigromaculata*. **17.** Living adult, 22 mm long, from Bahía Falsa, Baja California, May 2001. Included as a paratype of *Dendrodoris behrensi* by Millen and Bertsch (2005). **18.** Adult, no date or locality (Lance Collection, Species Folder: White Porostome Spotted). **19.** Egg mass, sketch labelled as South Casa Reef, La Jolla, 20 July 1974, but Lance Field Accounts indicate adults were from Hill Street, San Diego, 19 July 1974 (Lance Collection, Species Folder: White Porostome Spotted). **20.** Recently hatched juvenile, Aug. 1974 (pencil sketch in Lance Collection, Species Folder: White Porostome Spotted). **21.** Juvenile, 570 µm long, four days after hatching, June 2001. From egg mass laid by adult from Bahía Falsa, Baja California, May 2001 (Goddard 2005, as *Dendrodoris behrensi*).

*Dendrodoris behrensi* – Holotype: California, 14 Feb 1988 (CASIZ 69303). Paratypes: California, 14 Feb 1988 (CASIZ 171658); San Quintín, Mexico, 27 May 2001 (CASIZ 171659), San Quintín, Mexico, 27 May 2001 (CASIZ 171660).

**Anatomy:** The anatomy of *Dendrodoris nigromaculata* was described by Cockerell and Eliot (1905) and Millen and Bertsch (2005). As noted by Cockerell and Eliot (1905), Lance (Lance Collection, Species Folder: White Porostome Spotted), and Goddard (2005), notal spicules

are sparse and consist of straight to slightly curved rods only, some of which are irregular in outline (Figures 1, 20–21).

**External Morphology:** The external morphology of *D. nigromaculata* was described by Cockerell and Eliot (1905) and Millen and Bertsch (2005), with additional details presented by Lance (Lance Collection, Species Folder: White Porostome Spotted). Adults grow to 27 mm long and are distinguished externally by their translucent white ground color and chocolate brown blotches,

the larger of which are usually clustered into three or four groups centered mid-dorsally, and the smaller of which are scattered toward the edges of the dorsum (Figures 17–18).

**Development:** As described by Goddard (2005) and Lance (Lance Collection, Species Folder: White Porostome Spotted) *Dendrodoris nigromaculata* has a metamorphic direct development in short, stout egg ribbons laid on edge in a loose coil of only a turn or two (Figure 19). Juveniles (Figures 20–21) hatch after an embryonic period of 38 days at 16–19° C and are about 510 microns long.

**Geographic Distribution:** *Dendrodoris nigromaculata* is known from the Monterey Peninsula, California south to the San Benitos Islands, Baja California (McDonald, 1983; Behrens and Gatewood, 1986; Millen and Bertsch, 2005) (Figure 23).

**Remarks:** Bergh (1878) described the species *Doriopsis vidua* based on specimens collected from Tahiti, French Polynesia. The illustrations of the live animal (Bergh, 1878: pl. 1, figs. 17–20) represent an elongate *Dendrodoris* with a white background color and numerous black spots all over the dorsum, larger near the center of the animal, and small dorsal tubercles. Based on the body shape and coloration, *D. vidua* is most likely a senior synonym of *Dendrodoris elongata* Baba, 1936. Cockerel and Eliot (1905) tentatively reported this species from California as *Doridopsis vidua* (?), based on a single specimen collected



Figure 22. Map showing collection localities of *Doriopsilla rowena*.

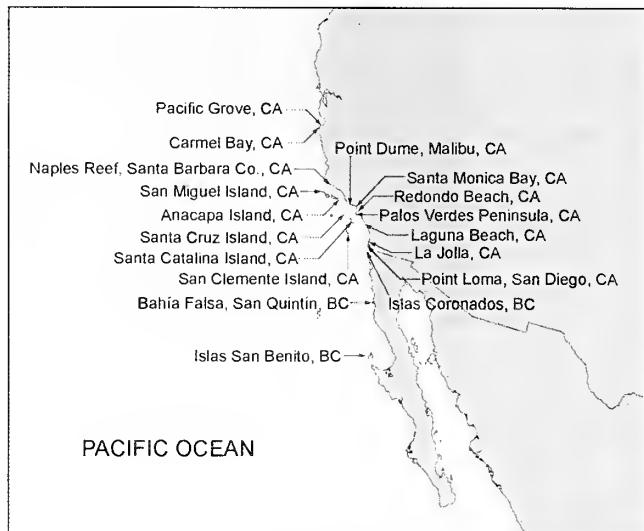


Figure 23. Map showing collection localities of *Dendrodoris nigromaculata*.

in La Jolla. Cockerel and Eliot (1905) noted some differences between their specimen and Bergh's (1878) original description in several details, including the coloration and mantle margin width. Cockerel and Eliot (1905) also indicated that their record was "suspicious" considering the geographic distance between the type locality and California, thus they introduced Cockerell's new name *Doridopsis nigromaculata* in case the specimen was ultimately proven to belong to a distinct species. As mentioned above, examination of the specimen studied by Cockerel and Eliot (1905) and therefore the holotype of *D. nigromaculata* (NHMUK 1904.7.7.1) revealed that it is a species of *Dendrodoris*. The holotype of *D. nigromaculata* has three pairs of large dark spots and several smaller spots irregularly distributed (Figure 1), very different from the original description of *Doriopsis vidua* by Bergh (1878) and references to *D. nigromaculata* by other authors, but nearly identical to the original description of *D. behrensi* by Millen and Bertsch (2005).

Lance was aware of this species as early as 1961 (or possibly even 1953) and referred to it in his notes and illustrations first as the "crenulate dorid," then as the "white dendrodorid" or "brown-spotted *Dendrodoris*" (Lance Collection, Species Folder: White Porostome Spotted), and in his field accounts as "*Dendrodoris* sp. true *dendrodoris*" (19 July 1974, Hill St) and "*Dendrodoris* sp. 3 [following Behrens 1991] white porostome" (26 Apr. 1998, So Casa Reef). As evidenced by an undated, handwritten description and pen and ink illustration of an adult (Figure 18), Lance started to formally describe it under the manuscript name "*Dendrodoris barbarensis*," based on five specimens collected in the 1950's and 60's from Naples Reef, Santa Barbara County; Point Loma, San Diego; and the Coronado Islands. Lance's folder for this species contains no evidence that he ever associated Cockerell and Eliot's (1905) description of *D. nigromaculata* with it.

F.M. MacFarland collected *D. nigromaculata* on the Monterey Peninsula in the 1920s (see Millen and Bertsch 2005, Material Examined). However, MacFarland (1966) does not mention those specimens nor refer to Cockerell and Eliot's 1905 description of *D. nigromaculata*.

## DISCUSSION

The taxonomic confusion surrounding *Dendrodoris nigromaculata* and *Doriopsilla rowena* likely has two main sources, the first being the historical controversy over the validity of Bergh's genus *Doriopsilla*, and the second being Lance's overlooking of Cockerell and Eliot's description of *Dendrodoris nigromaculata* as he was describing "Dendrodoris barbarensis." Lance was clearly familiar with Cockerell and Eliot's 1905 paper, and in hindsight their description of *Dendrodoris nigromaculata* is unequivocal, especially with respect to color pattern, so how could Lance have ended up misapplying that name to the smaller and differently colored species we have shown here to be *Doriopsilla rowena*? The type locality, combined with a view of habitat fidelity for nudibranchs, may be keys. After a decade of collecting along the coast of San Diego County Jim Lance considered himself intimately acquainted with the intertidal nudibranchs there (see Steinberg 1961: 59), and must have wondered why he had never found Cockerell's *D. nigromaculata* from 60 years earlier. Thus, in 1967 when Lance did find in La Jolla a dendrodoridid with brown spots that was new to him, he was primed to recognize it as Cockerell's missing *Dendrodoris nigromaculata*, overlooking that that name better applied to his "Dendrodoris barbarensis" which he had already seen from other locations in southern California. In any case, once Lance misapplied the name, new workers in the field followed his lead and considerable authority, especially with regards to the fauna of southern California (see Steinberg, 1961; Lance, 1961, 1966). The inertia gained by this use of *nigromaculata* subsumed *rowena* for decades among California workers, helped muddle the generic distinctions between *Dendrodoris* and *Doriopsilla*, and steered Millen and Bertsch (2005) away from considering Cockerell's *nigromaculata* when they described it as *Dendrodoris behrensi*. Cockerell's type specimen of *Dendrodoris nigromaculata* had effectively become a cold case, sitting on a shelf half a world away in the Natural History Museum in London, its type status unknown to the museum curatorial staff.

*Doriopsilla rowena* from the Pacific coast of California and Baja California lay large eggs and have ametamorphic direct development. However, based on the limited information presented by Goddard and Hermosillo (2008), members of the Panamic population appears to have planktotrophic development, which is consistent with a geographic range stretching from the northern Gulf of California to Panama and the Galapagos Islands. However, if planktotrophy is confirmed, including at the type locality of *D. rowena* in Puerto Peñasco, then

the directly developing population from California and the Pacific coast of Baja California likely represents an undescribed cryptic species. An alternative explanation is that this species displays poecilogeny. Aside from its rarity, there are no confirmed examples of poecilogeny that include such disparate modes of development, thus we consider the first hypothesis as the most likely. *Doriopsilla gemela* Gosliner, Schaefer, and Millen, 1999 exhibits a similar but geographically reversed variability, with planktotrophic development in California and direct development in the Gulf of California (Goddard, 2005; and see Lance Collection, Species Folder: Gulf Yellow Porostome), and has recently been found to comprise two species (Hoover et al., in preparation). Genetic confirmation of the two forms of *D. rowena* as separate species would bring the total number of nominal species of dendrodoridid nudibranchs in the greater region to eleven.

## ACKNOWLEDGMENTS

Terry Gosliner and Liz Kools (CASIZ) loaned us specimens collected by Jim Lance for examination and provided us access to the Lance Collection. Andreia Salvador (NHMUK) and Chris Meyer (USNM) provided us with photographs and information on the type specimens of *D. nigromaculata* and *D. rowena* respectively. Suggestions by Terry Gosliner and Sandra Millen improved the manuscript substantially.

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Natural History Museum  
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900 Exposition Boulevard  
Los Angeles, CA 90007

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# Paleocene and Miocene *Thyasira* sensu stricto (Bivalvia: Thyasiridae) from chemosynthetic communities from Japan and New Zealand

## Kazutaka Amano

Department of Geoscience  
Joetsu University of Education  
Joetsu 943-8512, JAPAN  
aman@juen.ac.jp

## Crispin T.S. Little

School of Earth and Environment  
University of Leeds  
Leeds LS2 9JT, UNITED KINGDOM  
earctsl@leeds.ac.uk

## Kathleen A. Campbell

Earth Sciences Programme  
School of Environment, Faculty of Science  
University of Auckland  
Private Bag 92019, Auckland Mail Centre  
Auckland 1142, NEW ZEALAND  
ka.campbell@auckland.ac.nz

## Robert G. Jenkins

School of Natural System  
College of Science and Engineering  
Kanazawa University  
Kanazawa City, Ishikawa  
920-1192, JAPAN  
robertgj@kanazawa-u.ac.jp

## Kristian P. Saether

State Key Laboratory of Palaeobiology and Stratigraphy  
Nanjing Institute of Geology and Palaeontology  
39 Beijing East Road  
Nanjing 210008, CHINA  
kris.saether@nigpas.ac.cn

## ABSTRACT

A new species of bivalve, *Thyasira* (*Thyasira*) *beui*, is described from lower to middle Miocene hydrocarbon seep deposits from the North Island of New Zealand. *Thyasira* (*T.*) *nakazawai* Matsumoto, 1971 is redescribed from lower Miocene seep deposits in central Honshu of Japan, and *T.* (*T.*) sp. from Paleocene wood-fall communities in eastern Hokkaido is described as the first *Thyasira* sensu stricto of this age in Japan. As the genus *Conchocele* replaced the niche of *Thyasira* sensu stricto at seep sites from the Eocene in Japan, the occurrence of *T.* (*T.*) *nakazawai* is an exceptional occurrence of this genus at younger seeps in Japan. In contrast, *Conchocele* disappeared from New Zealand waters from the end of the Paleocene, leaving *Thyasira* sensu stricto as the sole thyasirid taxon at New Zealand Cenozoic seep sites.

**Additional Keywords:** *Conchocele*, Fossil, hydrocarbon seep, cold seep

## INTRODUCTION

Bivalves within the family Thyasiridae today inhabit reduced environments from intertidal mudflats to deep-sea hydrothermal vents. Some thyasirid species host chemoautotrophic bacteria in their gills, particularly those toward the larger end of the size range of the family, and some do not (Dufour, 2005; Oliver and Levin, 2006; Taylor and Glover, 2010). Most species within the genus *Thyasira* have two demibranchs

and symbionts (Oliver and Killeen, 2002; Dufour, 2005). Such chemosymbiotic thyasirids are deep burrowers and mine sulfide deep in the substrate using their vermiform foot (Dando and Southward, 1986; Seilacher, 1990; Oliver and Killeen, 2002; Dufour and Felbeck, 2003). Thyasirid species can extend their foot up to 30 times the length of the shell (Dufour and Felbeck, 2003).

The oldest known thyasirid, *Cretaxinus hurumi* Hryniewicz, Little, and Nakrem, 2014, comes from uppermost Jurassic to lowermost Cretaceous seeps in Svalbard. As noted by Kiel et al. (2008), *Thyasira rouyana* (d'Orbigny, 1844) from Lower Cretaceous (Valangian–Hauterivian) rocks in Europe is the oldest species of *Thyasira* sensu stricto. By the late Early Cretaceous (Albian), species within this subgenus appeared in seep sites in Hokkaido, northern Japan (Kiel et al., 2008, 2009).

Several species of *Thyasira* sensu stricto have been reported from Cenozoic deposits around the Pacific Rim (Table 1), including *Thyasira* sensu stricto from Paleocene carbonates with plant debris in eastern Hokkaido, Japan, *Thyasira nakazawai* from Miocene accretionary-prism deposits in central Honshu, Japan (Matsumoto, 1971), and *Thyasira* sp. from Miocene seep deposits of North Island, New Zealand (Campbell et al., 2008).

Here we formally describe *Thyasira* sensu stricto fossils from the Paleocene and Miocene of Japan and the Miocene from New Zealand. The descriptions extend knowledge of the fossil species of *Thyasira* sensu stricto

**Table 1.** Cenozoic *Thyasira* sensu stricto from the Pacific Rim. Symbols: \* maximum length (mm); \*\* length > height; + distinctly longer than high, ± subcircular, – distinctly higher than long; \*\*\* medial flattened area.

Species	Country, District	Age	Max L*	L>H**	MF***	Data source
<i>Thyasira</i> ( <i>Thyasira</i> ) sp.	Hokkaido, Japan	Paleocene	10.1	+	–	This study
<i>T. (T.) baca</i> Devjatilova, 1981	Kamchatka, Russia	Paleocene	13	–	–	Devjatilova and Volobueva (1981)
<i>T. (T.) mironovi</i> Kalishevich, 1981	South Sakhalin, Russia	Paleocene	12	±	+?	Kalishevich et al. (1981)
<i>T. (T.) uncinata</i> Kalishevich, 1981	South Sakhalin, Russia	Paleocene	14	+	–	Kalishevich et al. (1981)
<i>T. (T.) xylodgia</i> Kiel and Goedert, 2007	Washington, USA	Latest Eoc.–e. Oligoc.	21	?	–	Kiel and Goedert (2007)
<i>T. (T.) peruviana</i> Olsson, 1931	Peru	Oligocene	25	±	–	Olsson (1931)
<i>T. (T.) nakazawai</i> Matsumoto, 1971	central Honshu, Japan	E. Miocene	28.3	+	–	Matsumoto (1971)
<i>T. (T.) minoensis</i> Itoigawa, 1960	central Honshu, Japan	E. Miocene	14.1	–	+	This study
<i>T. (T.) motutaraensis</i> Powell, 1935	North Is., New Zealand	E. Miocene	6.5	–	–	Powell (1935)
<i>T. (T.) bartrumi</i> Powell, 1935	North Is., New Zealand	E. Miocene	15	+	+	Powell (1935)
<i>T. (T.) beui</i> new species	North Is., New Zealand	E.–m. Miocene	13.8	+	–	This study
<i>T. (T.) nana</i> Khomenko, 1929	Kamchatka, Sakhalin, Russia	M. Miocene	6	+	–	Khomenko (1929)
<i>T. (T.) marwicki</i> nom. nov.	North Is., New Zealand	L. Miocene	10	+	–	Marwick (1926), as <i>Thyasira planata</i>
<i>T. (T.) tokunagai</i> Kuroda and Habe, 1951	Japan	E. Miocene–rec.	13.6	–	+	This study
<i>T. (T.) gouldii</i> (Philippi, 1845a)	California, USA	Pliocene–rec.	12	–	+	Oekelmann (1958), Coan et al. (2000)
<i>T. (T.) peregrina</i> (Iredale, 1930)	New Zealand	Pliocene–rec.	10.4	–	+	This study
<i>T. (T.) ozawai</i> (Yokoyama, 1926)	Japan	E. Pleistocene	15.3	–	+	This study

in hydrocarbon seep and wood-fall communities from the Pacific Rim.

## MATERIALS AND METHODS

The fossils used in this study were collected from two Paleocene sites in Japan and from two Miocene localities in New Zealand. We also examined some Miocene specimens from New Zealand housed at the University of Auckland and one Miocene species described by Matsumoto (1971), which is stored at National Museum of Nature and Science, Tokyo. Details of localities and associated faunas are as follows:

**Eastern Hokkaido, Japan.** All specimens were collected from two carbonate float blocks from the Katsuhira-zawa (K1) and Katsuhira-kita-zawa (K2) localities of Urahoro Town, eastern Hokkaido, Japan (Figure 1). The upper part of the Katsuhira Formation crops out in this area and consists of mudstones yielding carbonates that contain many plant fragments. The carbonates containing the thyasirid fossils have probably been eroded out from the mudstones of this formation, the age of which has been assigned to the Paleocene (early Selandian)

(see Amano and Jenkins, 2014). In addition to the thyasirid bivalves, the carbonates also contain specimens of a provannid(?) gastropod, a limpet, and *Bentharca steffensi* (Amano et al., 2015). The taxonomic composition of this fauna suggests that its primary energy source was the degradation products derived from sunken wood, which was probably bored by xylophagain bivalves.

**Central Honshu, Japan.** *Thyasira nakazawai* Matsumoto, 1971 was the name proposed for specimens collected from limestone lenses or calcareous mudstones within turbidites of the Wappazawa Formation (Setogawa Group) on a branch of the Hakkou River, 1600 m west of Matsushita, Shimada City (S1) and at Nakadaira, Shimada City (S2) (Figure 1). The age of the Wappazawa Formation has been assigned to the early Miocene (Watanabe, 1988). From the formation, molluscan fossils have been recovered only from the limestone lenses and calcareous mudstones (Matsumoto, 1971). *Thyasira nakazawai* was collected with *Saxolucina (Megaxinus) matsushitai* Matsumoto, 1971 and *Pitar matsuensis* (Nagao, 1928) [= *Pliocardia?* sp.]. Based on the fauna and lithofacies of the limestone lenses and calcareous mudstones, the taxa from these localities probably inhabited hydrocarbon seeps.

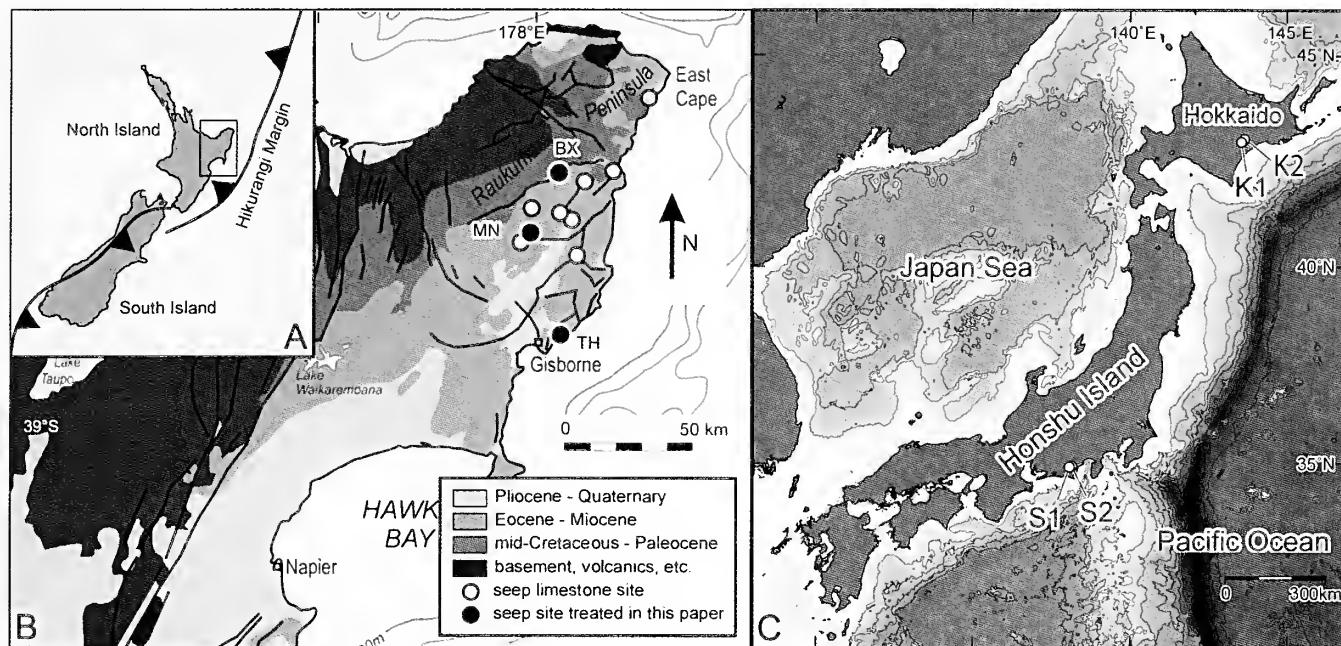


Figure 1. Localities of the fossil *Thyasira* sensu stricto described herein.

**North Island, New Zealand.** Specimens of *Thyasira beui* new species were collected from hydrocarbon seep carbonates from the Moonlight North (MN), Bexhaven (BX), and Turihaua (TH) localities, north of Gisborne, North Island, New Zealand (Figure 1). The deposits belong to the Bexhaven Limestone, which is assigned to the early to middle Miocene (Campbell et al., 2008). From MN, Amano et al. (2014) described the vesicomyid species *Notocalyptogena neozelandica* and *Pliocardia*? sp. Saether et al. (2010) described the bathymodioline mussels, *Bathymodiolus* (s. l.) *heretaunga*, from BX and MN, and *Gigantidus coseli* from BX, MN, and TH.

We describe the *Thyasira* species in this study using the terminology of Kauffman (1967) and Oliver and Killeen (2002). All figured and supplementary specimens are catalogued at the University of Auckland (UOA L), Joetsu University of Education (JUE) and the National Museum of Nature and Science (NSM).

#### SYSTEMATIC PALEONTOLOGY

Family *Thyasiridae* Dall, 1900 (Dall, 1895)

Genus *Thyasira* Lamarck, 1818

Subgenus *Thyasira* Lamarck, 1818

**Type Species:** *Tellina flexuosa* Montagu, 1803

**Remarks:** The subgenus *Parathyasira* Iredale, 1930 differs from *Thyasira* sensu stricto by having no shell auricle. Most historical and some recent literature has treated the taxon *Conchocele* as a subgenus of *Thyasira* (e.g., Yabe, H. and S. Nomura, 1925; Grant and Gale, 1931; Krishtofovich, 1936; Slodkewitsch, 1938; Weaver, 1942;

Hickman, 1984; Matsui, 1985; Moore, 1988; Matsui, 1990). However, *Conchocele* Gabb, 1866 attains a large size (max. 165.4 mm in length; Kamenev et al., 2001), has a thick shell, and lacks an auricle. Therefore, we regard *Conchocele* as a genus distinct from *Thyasira*.

***Thyasira* (*Thyasira*) *nakazawai* Matsumoto, 1971**  
(Figures 2–7)

*Thyasira nakazawai* Matsumoto, 1971: 665–666, pl. 3, fig. 15–18, Amano, 2014: 7, fig. 1.

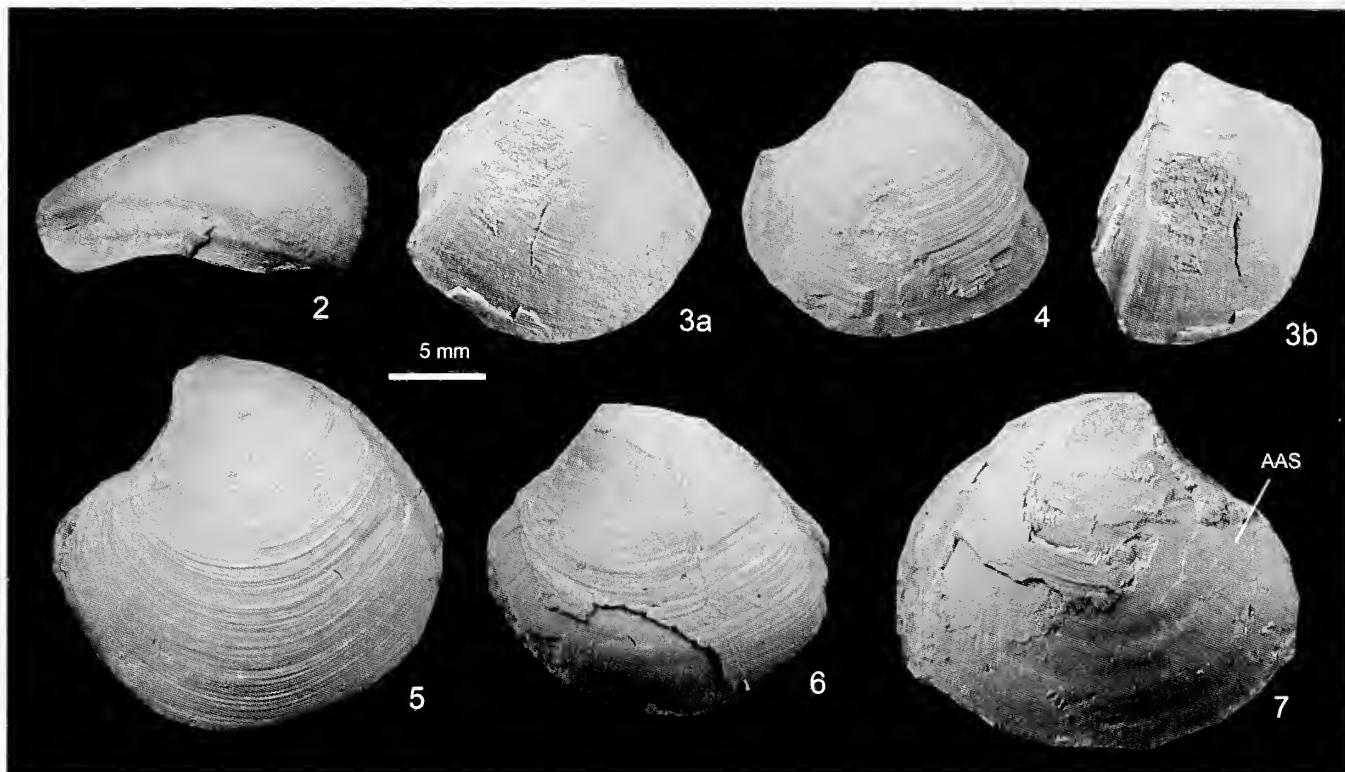
**Type Material:** Holotype, NSM PM-16922a. Paratypes, NSM PM-16923, NSM PM-16924, NSM PM-16925.

**Material Examined:** Eleven specimens including the type specimens.

**Measurement:** See Table 2.

**Original Description:** “Shell medium in size, thin triangular oval, nearly long as high, strongly inflated. Antero-dorsal border strongly concave, sharply turned to broadly curved, subangular ventral border forming almost a right angle; postero-dorsal long, faintly arched passing into the ventral border forming an obtuse angle. Beak small, strongly curved forward and situated at about the middle of the shell. Surface of the shell ornamented with fine and concentric, but somewhat irregular growth-lines. Posterior surface depressed from the upper side of the postero-ventral corner making oblique ridge. A central part of the shell faintly ridged from the beak to middle of the ventral border.”

**Complementary Description:** On examination of the material we found that there are some elements of the



**Figures 2–7.** *Thyasira (Thyasira) nakazawai* Matsumoto. 2. Dorsal view of posterior part of left valve; Paratype; NSM PM-16924; Loc. S1. 3a, b. Frontal and oblique view of right valve; NSM PM-16910; Loc. S2. 4. Frontal view of left valve; Paratype; NSM PM-16923; Loc. S1. 5. Frontal view of left valve; Holotype; NSM PM-16922a; Loc. S1. 6. Frontal view of left valve; NSM PM-16905; Loc. S1. 7. Inner surface of right valve; AAS, anterior adductor scar; NSM PM-16909; Loc. S1.

**Table 2.** Measurements of *Thyasira (Thyasira) nakazawai* Matsumoto.

Number of specimens	Type	Length (mm)	Height (mm)	Width (mm)	H/L	W/L	Valve
NSM PM-16922a	Holotype	20.6	19.1	-	0.93	-	left
NSM PM-16923	Paratype	14.9	13.1	-	0.88	-	left
NSM PM-16924	Paratype	15.5+	13.8	-	-	-	left
NSM PM-16925	Paratype	18.5	16.9	-	0.91	-	right
NSM PM-16905		16.2	16.7	-	1.03	-	right
NSM PM-16906		22.0	20.1	15.5	0.91	0.70	both
NSM PM-16908		17.9	17.5	-	0.98	-	left
NSM PM-16909		20.4	17.3	-	0.85	-	right
NSM PM-16910-1		21.0	18.4	-	0.88	-	left
NSM PM-16910-2		16.0	15.5	-	0.97	-	right

original description of the species that are incorrect. We therefore offer here more accurate and complementary morphological information.

Shell rather large for the genus (maximum 28.3 mm in length), thin, ovate, slightly longer than high (height/length ratio = 0.85–0.97; exceptionally 1.03), well inflated (width/length ratio = 0.70). Anterodorsal margin short, strongly concave; anterior margin subcircular and graduating into arched ventral margin. Second posterior fold distinct, but not stronger than first posterior fold; posterior sulcus rather shallow and narrow; first posterior fold strong and ridged; submarginal sulcus distinct;

auricle narrow but extending total length of submarginal sulcus. Lunule moderately depressed. Beak prominent, prosogyrate, situated at about one-third of shell length. Shell surface ornamented with fine growth lines. Anterior adductor scar elongate quadrate and attached to pallial line; posterior adductor scar indistinct. Inner surface of shell crenulated by many fine radial lines.

**Comparison:** *Thyasira (Thyasira) nakazawai* is similar to *T. (T.) tanabei* Kiel, Amano and Jenkins, 2008 from the Upper Cretaceous formations in Hokkaido, sharing a strongly concave anterodorsal margin and strong and

ridged posterior fold. However, *T. (T.) nakazawai* differs from the latter species by having a larger (maximum length of *T. (T.) tanabei* = 13.5 mm) and more inflated shell with a smaller anterior adductor scar.

**Distribution:** Lower Miocene Wappazawa Formation of the Setogawa Group from the Shizuoka Prefecture, central Honshu, Japan.

***Thyasira (Thyasira) beui* new species**  
(Figures 8–15)

*Thyasira* sp.—Campbell et al., 2008: 90.

*Thyasira* sp. nov.—Saether, 2011: 135–138, fig. 5–19.

**Diagnosis:** Medium-sized *Thyasira* with suborbicular shell, shallow lunule, and small auricle. Ventral end of first posterior fold occasionally angulated.

**Description:** Shell up to 13.8 mm in length, rather thin, moderately inflated (width/length ratio = 0.58–0.91), suborbicular (height/length ratio = 0.90–1.17), equivalve and inequilateral. Antero-dorsal margin broadly arched and continuing to rounded anterior margin; ventral margin broadly arched. Auricle small, extending in length two-thirds along marginal sulcus; first posterior fold sharp, with ventral end occasionally angulated; posterior sulcus very shallow; second posterior fold less distinct than first posterior fold. Beak prominent, prosogyrate and located around two-fifths of shell length (i.e., at 36–44% of shell length from anterior margin). Lunule shallow and demarcated by very shallow groove. Shell surface with fine growth lines. Inner shell surface ornamented by many fine radial grooves. Pallial line entire, starting from midpoint of ventral side of anterior adductor scar. Anterior adductor scar elongate-quadrata; posterior adductor scar very small and ovate.

**Holotype:** UOA L4626 from MN (Y16/f1054), collection AU 15844.

**Paratypes:** UOA L4627 from MN (Y16/1033), collection AU 19618; UOA L4628 from MN (Y16/f1174), collection AU 19923; UOA L4629 and L4630 from MN (Y16/1059), collection AU 19982; UOA L4631 from BX (Y16/1032), collection AU 19617.

**Type Locality:** Moonlight North seep carbonates, north of Gisborne, North Island, New Zealand.

**Material Examined:** Twenty-two specimens from three localities (Loc. MN, BX, TH in Figure 1).

**Measurements:** See Table 3.

**Remarks:** *Thyasira (Thyasira) beui* is *Thyasira* sp. in the compilation of molluscan fossils (in part taken from Beu and Maxwell (1990)) from New Zealand hydrocarbon seep carbonates in Campbell et al. (2008). Saether (2011) described and illustrated this species as “*Thyasira* sp. nov.” in his unpublished Ph.D. thesis.

**Comparison:** *Thyasira (Thyasira) beui* shares a prominent beak and a moderately inflated shell with *T. (T.) motutaraensis* Powell, 1935 from the lower Miocene Motutara deposit west of Auckland, North Island, New Zealand (see also Beu and Maxwell, 1990). However, *T. (T.) motutaraensis* can be separated from the new species by its smaller and higher triangular shell (length = 7.4 mm, height/length ratio = 1.14). *Thyasira (T.) planata* Marwick, 1926 [this name was preoccupied by Jeffreys, 1882 and a new name, *T. (T.) marwicki* is proposed herein] from upper Miocene deposits in the western part of North Island, New Zealand, can be distinguished from *T. (T.) beui* by having a wider posterior area, a longer marginal sulcus, and a narrower auricle than that of the new species. *Thyasira (T.) mironovi* Kalishevich from the Paleocene of South Sakhalin (Klishevich et al. 1981) is similar to *T. (T.) beui* in having a first posterior fold with angular ventral end. However, *T. (T.) mironovi* can be separated from *T. (T.) beui* by having a less inflated shell, a wider posterior fold and a weak medial flattened area. Another species from the Paleocene of South Sakhalin, *T. (T.) uncinata* Kalishevich, can be easily distinguished from *T. (T.) beui* by having an elongate shell with posteriorly situated beak. *Thyasira (T.) bartrumi* Powell, 1935 from the lower Miocene Motutara deposit is distinctly different from *T. (T.) beui* by having a *Conchocele*-like shell with beak at anterior one-seventh of shell length and a medial flattened area. The Recent New Zealand species, *T. (T.) peregrina* Iredale, 1930 differs from *T. (T.) beui* by its smaller shell (maximum length = 10.4 mm), which is higher than long, and by having a medial flattened area.

**Distribution:** Lower to middle Miocene Bexhaven Limestone, north of Gisborne, North Island, New Zealand.

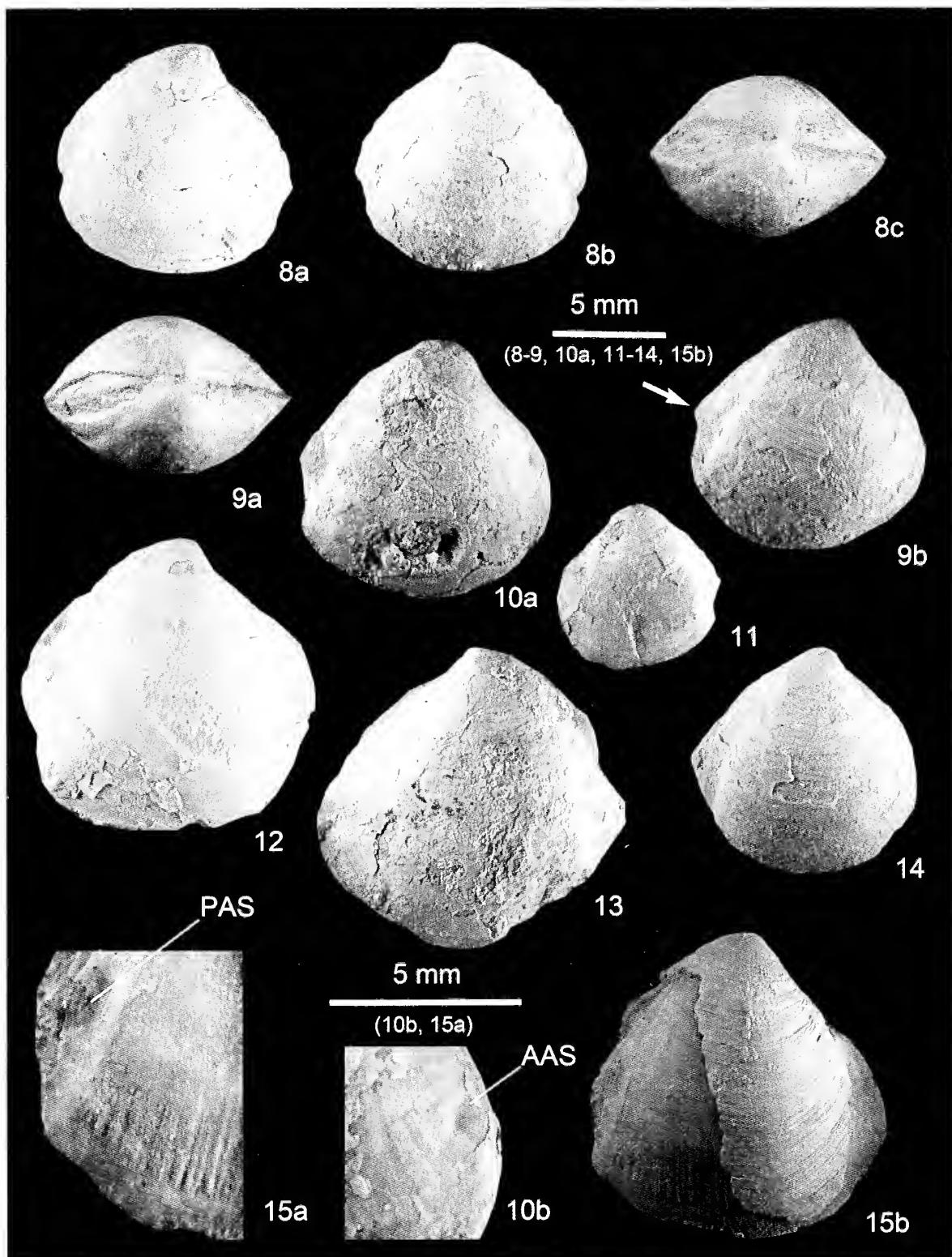
**Etymology:** Named after Dr. Alan G. Beu who has made significant contributions to the taxonomy of Cenozoic fossil faunas from New Zealand.

***Thyasira (Thyasira) sp.***  
(Figures 16–17)

**Material Examined:** Two articulated but imperfect specimens (JUE nos. 15936, 15937).

**Description:** Shell rather small in size (9.7–10.1 mm + in length), thin, ovate, longer than high, well inflated (width/length ratio = 0.52–0.58). Anterodorsal margin short, nearly straight; anterior margin subcircular. Second posterior fold distinct; posterior sulcus rather deep; first posterior fold wide and ridged; submarginal sulcus distinct; auricle narrow and short. Beak prosogyrate. Inner structure of shell not preserved.

**Comparison:** *Thyasira (Thyasira)* sp. is similar to the Cretaceous species, *T. (T.) tanabei* Kiel, Amano and Jenkins, 2008 by having a ridged first posterior fold. However, the wide posterior area of our specimens enables us to separate *T. (T.)* sp. from *T. (T.) tanabei*.



**Figures 8–15.** *Thyasira (Thyasira) beui* new species. All specimens except for one illustrated in Figure 15a, b are from the type locality (Moonlight North; MN). One specimen of Figure 15a, b is from Bexhaven (BX). **8a–c.** Frontal and dorsal views of both valves; Paratype; UOA L4629. **9a, b.** Frontal view of right valve and dorsal view of both valves; Holotype; UOA L4626; white arrow showing an angulated ventral end of first posterior fold. **10a, b.** Inner surface of right valve and its enlargement of the area around AAS (= anterior adductor scar); Paratype; UOA L4630. **11.** Frontal view of left valve; Paratype; UOA L4628. **12.** Frontal view of right valve; UOA L4638. **13.** Frontal view of left valve; left valve; UOA L4640. **14.** Frontal view of right valve; UOA L4627. Inner surface of right valve showing PAS (= posterior adductor scar) and its enlargement; Paratype; UOA L4631.

**Table 3.** Measurements of *Thyasira (Thyasira) beui* new species.

Number of specimens	Type	Length (mm)	Height (mm)	Width (mm)	H/L	W/L	Valve	Collection Number	Locality Number
UOA L4626	Holotype	10.2	9.6	6.6	0.94	0.65	both	AU15844	Y16/f1054
UOA L4627	Paratype	10.3	10.2	6.6	0.99	0.64	both	AU19618	Y16/f1033
UOA L4628	Paratype	7.2	7.4	-	1.03	-	left	AU19923	Y16/f1174
UOA L4629	Paratype	9.5	10.4	7.1	1.09	0.75	both	AU19982	Y16/f1059
UOA L4630	Paratype	10.4	10.3	7.0	0.99	0.67	both	AU19982	Y16/f1059
UOA L4631	Paratype	12.4	12.9	9.3	1.04	0.75	both	AU19617	Y16/f1032
UOA L4632		14.8	14.7	10.7	0.99	0.72	both	AU15844	Y16/f1054
UOA L4633		10.5	11.3	7.3	1.08	0.70	both	AU15844	Y16/f1054
UOA L4634		12.7	13.4	9.7	1.06	0.76	both	AU15844	Y16/f1054
UOA L4635		9.2	9.1	-	0.92	-	left	AU19872	Y16/f1048
UOA L4636		11.2	11.0	7.9	0.98	0.71	both	AU19922	Y18/f657
UOA L4637		11.1	10.0	8.0	0.90	0.72	both	AU19922	Y18/f657
UOA L4638		12.9	12.5	-	0.97	-	right	AU19923	Y16/f1174
UOA L4639		9.0	8.1	-	0.90	-	right	AU19923	Y16/f1174
UOA L4640		13.8	12.7	-	0.92	-	left	AU19982	Y16/f1059
UOA L4641		10.7	10.9	7.4	1.02	0.69	both	AU19982	Y16/f1059
UOA L4642		10.2	11.9	9.3	1.17	0.91	both	AU19982	Y16/f1059
UOA L4643		12.0	12.1	7.9	1.01	0.66	both	AU19982	Y16/f1059
UOA L4644		12.6	12.3	9.2	0.98	0.73	both	AU19982	Y16/f1059
UOA L4645		7.6	7.7	4.6	1.01	0.61	both	AU19982	Y16/f1059

*T. (T.) xylodia* Kiel and Goedert, 2007 comes from latest Eocene and early Oligocene wood-fall communities in Washington State, USA and can be distinguished from *T. (T.)* sp. by its larger size (21 mm in length), deeply concave antero-dorsal margin and narrower posterior area. *T. (T.) baca* Devyatilova from the Paleocene Getklninskaya Formation of western Kamchatka (Devyatilova and Volobueva, 1981) differs from *T. (T.)* sp. by having a triangular shell and narrower posterior area. *Thyasira (T.) mironovi* Kalishevich can be distinguished from *T. (T.)* sp. by having wider first posterior fold with an angular ventral end and extending its ventral end to the ventral margin of main disc.

**Distribution:** Paleocene, upper part of the Katsuhira Formation, eastern Hokkaido, Japan.

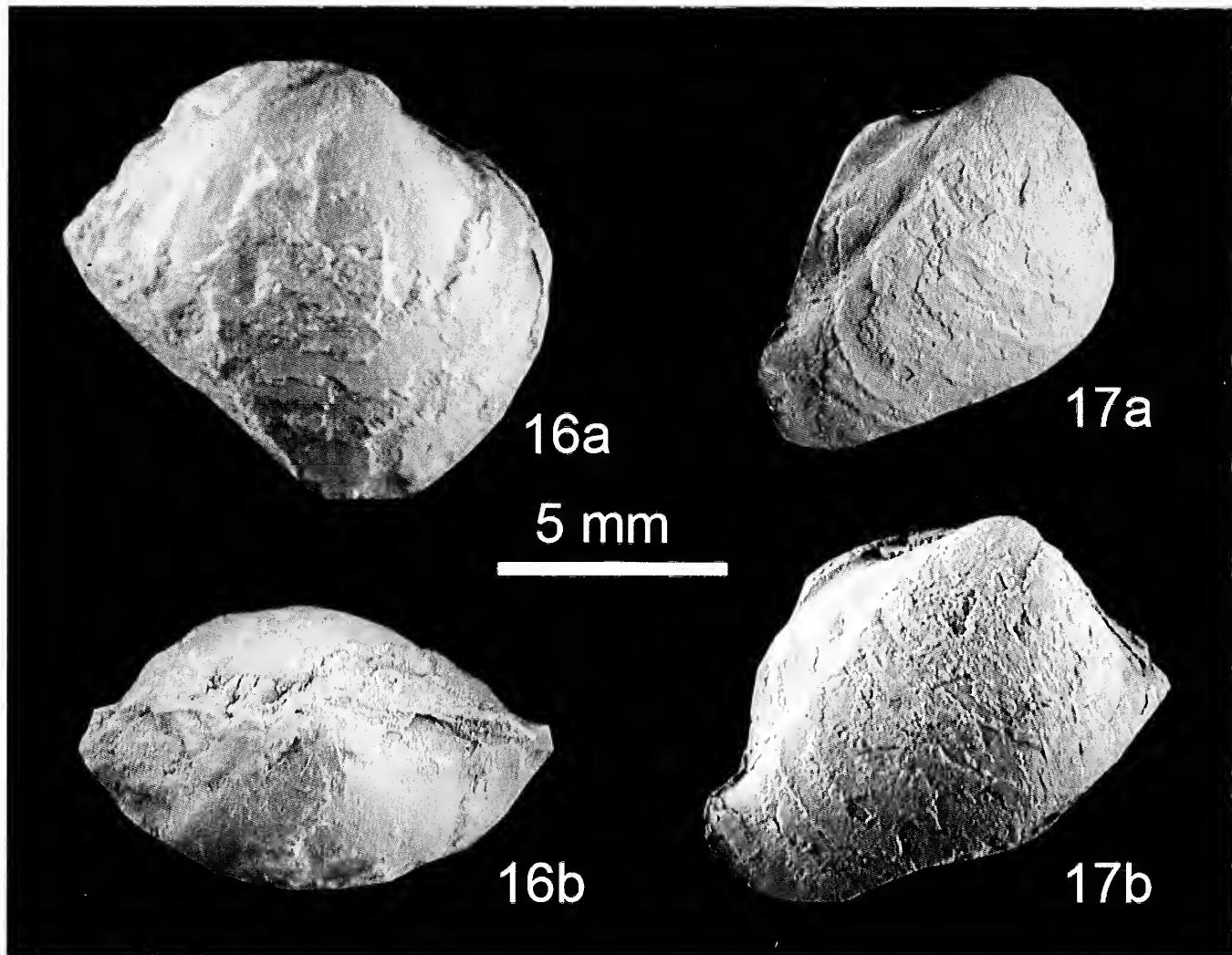
## DISCUSSION

Several Recent species of *Thyasira* sensu stricto have been recorded from hydrocarbon seep or hydrothermal vent sites (Table 4; Clarke, 1989; Dando et al., 1994; Oliver and Killeen, 2002; Olu et al., 2004; Oliver and Sellanes, 2005; Oliver and Holmes, 2006; Rodrigues et al., 2008). Based on recent molecular analysis of nuclear 18S rRNA and 28S rRNA, the subgenus *Thyasira* sensu stricto is divided into two clades (Taylor et al., 2007). *Thyasira (T.) sarsi* (Philippi, 1845b) and *T. (T.) methanophila* Oliver and Sellanes, 2005, from hydrocarbon seeps, form a monophyletic clade. *Thyasira sarsi* itself is an opportunistic species which is also able to live in sediments with low organic content, and at relatively low densities (Keuning et al., 2011). Another clade includes *T. (T.) flexuosa* (Montagu, 1803), *T. (T.) gouldii* (Philippi, 1845a), and *T. (T.) polygonata* (Jeffreys, 1864), none of which have

been recorded from seep and vent sites. Morphologically, the *T. (T.) sarsi*-*T. (T.) methanophila* clade differs from the *T. (T.) flexuosa*-*T. (T.) gouldii*-*T. (T.) polygonata* clade by having larger (more than 20 mm in length), subcircular or a slightly longer shells, without a medial flattened area. Other *Thyasira* species found in seep and vent sites, such as *T. (T.) southwardae* Oliver and Holmes, 2006, *T. (T.) vulcolutre* Rodrigues and Oliver in Rodrigues et al., 2008 and *T. (T.) oleophila* Clarke, 1989, also have similar shell characteristics to the *T. (T.) sarsi*-*T. (T.) methanophila* clade.

Payne and Allen (1991) and Dufour (2005) have shown that in thyasirids demibranch number is related to body size, because symbiotic thyasirids with only one demibranch only have access to a small amount of nutrients at bathyal depths. All the species discussed above have two demibranchs and chemosynthetic bacteria (Dufour, 2005; Oliver and Sellanes, 2005; Oliver and Holmes, 2006; Rodrigues and Oliver, 2008). Almost certainly because of the abundant supply of hydrogen sulfide at seep and vent sites, thyasirids living there can grow to large sizes relative to thyasirids inhabiting other environments. However, the reason that the thyasirids living in chemosynthetic environments have subcircular or longer shells, without a medial flattened area, is unknown. There are exceptions, as *T. (T.) striata* (Sturany, 1896), found at a Mediterranean seep by Olu et al. (2004), is characterized by a rather small (ca. 7.5 mm) and higher shell with a medial flattened area. This morphological information from Recent seep and vent *Thyasira* sensu stricto can be used to infer the paleoecology of fossil *Thyasira* sensu stricto species.

As shown in Table 1, *Thyasira (T.) nakazawai* has a large (length = 28.3 mm) and longer shell (height/length ratio = 0.85–0.97) without a medial flattened area,



**Figures 16–17.** *Thyasira (Thyasira) sp.* 16a, b. Frontal view of right valve and dorsal view of both valves; JUE no. 15936; Loc. K1. 17a, b. Frontal and oblique view of right valve; JUE no. 15937; K2.

**Table 4.** Morphology of recent species of *Thyasira* sensu stricto. \* maximum length (mm); \*\* Length>Height; + distinctly longer than high, ± subcircular, – distinctly higher than long; \*\*\* Medial flattened area.

Species	sites	Max L*	L>H**	MF***	Data source
<i>Thyasira (Thyasira) sarsi</i> (Philippi, 1845b)	seep	25	±	–	Dando et al. (1994), Oliver and Killeen (2002)
<i>T. (T.) methanophila</i> Oliver and Sellanes, 2005	seep	29.7	+	–	Oliver and Sellanes (2005)
<i>T. (T.) southwardae</i> Oliver and Holmes, 2006	vent	16.7	+	–	Oliver and Holmes (2006)
<i>T. (T.) vulcolatre</i> Rodrigues and Oliver, 2008	seep	17.2	±	–	Rodrigues et al. (2008)
<i>T. (T.) oleophila</i> Clarke, 1989	seep	ca.23	±	–	Clarke (1989)
<i>T. (T.) striata</i> (Sturany, 1896)	seep	ca.7.5	–	+	Olu et al. (2004)
<i>T. (T.) tokunagai</i> Kuroda and Habe, 1951	non-seep	13.6	–	+	This study
<i>T. (T.) gouldii</i> (Philippi, 1845a)	non-seep	12	–	+	Killeen and Oliver (2002b)
<i>T. (T.) polygonata</i> (Jeffreys, 1864)	non-seep	9	–	+	Killeen and Oliver (2002a)
<i>T. (T.) flexuosa</i> (Montagu, 1803)	non-seep	12	–	+	Oliver and Killeen (2002)

compared to *Thyasira* sensu stricto species from Cenozoic deposits around the Pacific Rim. Because of this, we speculate that *T. (T.) nakazawai* might have lived in cold seep areas. In contrast, *T. (T.) minoensis* Itoigawa,

1960 was collected from non-seep sandstones of the lower Miocene Oidawara Formation; it has a smaller (length = 14.1 mm) and higher shell (height/length ratio = 1.08) and with a distinct medial flattened area.

While the maximum size of *T. (T.) beui* new species is not large (length = 13.8 mm), the species has a suborbicular shell (height/length ratio = 0.90–1.17) without a medial flattened area. The carbonates and associated fauna (see also Campbell et al., 2008) indicate this species also thrived at fossil seep sites. Judging from the lithofacies and the associated fauna of limpets and provannids, the Paleocene *T. (T.)* sp. collected from eastern Hokkaido might have been a member of a fossil wood-fall community. Despite the small size of *T. (T.)* sp. (length = 9.7–10.1 mm) compared with other seep species, it also is longer than high and has no medial flattened area. Such small thyasirid species also have been recognized in Late Cretaceous wood-fall communities with limpets and provannids by Kiel et al. (2009). In the northern Pacific area, *Thyasira* sensu stricto occurred in hydrocarbon seeps and wood-fall sites during the Late Cretaceous (Kiel et al., 2008, 2009). The eastern Hokkaido Paleocene *Thyasira* sensu stricto species might have lived in wood-fall communities. The first large thyasirid, *Thyasira townsendi* (White, 1890) (almost certainly a species of *Conchocele*) appeared in Maastrichtian seep deposits of Snow Hill Island, Antarctica (Kiel et al., 2008; Little et al. 2015). The second oldest large thyasirid species, *Conchocele* aff. *conradi* (Rosenkrantz, 1942), is from the Danian Kangilia Formation of western Greenland (Rosenkrantz, 1970; Amano, 2014). From North Island, New Zealand, one specimen of *Conchocele* sp. has been recorded from Paleocene deposits at Angora Road, south of Wimbledon (Beu and Maxwell, 1990; Beu, 2014 personal communication). Another Paleocene *Conchocele* specimen up to 70 mm in length was collected from 1 km south of Te Kaukau Point, White Rock, South Wairarapa coast (Beu, 2014 personal communication). So far, no fossil *Conchocele* has been recorded from Paleocene deposits in the northern Pacific area.

Since the Eocene, the genus *Conchocele* seems to have replaced the niche of *Thyasira* sensu stricto in the northern Pacific. Lots of literature has described the radiation of *Conchocele* in Eocene to Recent times in this region (e.g., Yabe and Nomura, 1925; Grant and Gale, 1931; Krishtofovich, 1936; Slodkewitsch, 1938; Weaver, 1942; Hickman, 1984; Moore, 1988; Kamenev et al., 2001). *Conchocele* was also found from Eocene to Holocene seep sites and in Oligocene to Miocene whale-fall sites (Goedert et al., 1995; Majima et al., 2005; Amano et al., 2007; Kiel and Goedert, 2006). Thus the occurrence of *Thyasira* (*Thyasira*) *nakazawai* from lower Miocene seep deposits is an exceptional post-Eocene occurrence of *Thyasira* (*Thyasira*) species in the northern Pacific area. In contrast, in New Zealand *T. (T.) beui* occurs in lower to middle Miocene seep sites, in the absence of *Conchocele* from the region.

*Conchocele* might have migrated from western Greenland to the northern Pacific area (including Japan) by the Eocene (Amano and Jenkins, 2014), and once there to have replaced *Thyasira* sensu stricto because of its tolerance to lower oxygen environments. In New Zealand waters, in contrast, *Conchocele* did not

invade hydrocarbon seep sites and had disappeared from the region by end of the Paleocene. Thyasirids (probably *Thyasira* sensu stricto) from New Zealand Cretaceous seep deposits (Kiel et al., 2013) show that small sized thyasirids have flourished in the area since that time period.

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# A revision of the fossil taxa assigned to *Hyperaulax* (Gastropoda: Odontostomidae), with the description of a new genus (Gastropoda: Bulimulidae)

Kurt Auffenberg<sup>1</sup>

John Slapcinsky

Roger W. Portell

Florida Museum of Natural History  
University of Florida  
P.O. Box 117800  
Gainesville, FL 32611 USA

## ABSTRACT

Orthalicoid terrestrial snails recorded from the lower Miocene portion of the upper Oligocene to lower Miocene Tampa Member of the Arcadia Formation (Hawthorn Group) of southern Florida and the lower Miocene St. Marks Formation of northern Florida are reviewed. These taxa, previously allocated to the genus *Hyperaulax* Pilsbry, 1897 (Odontostomidae), are reassigned to *Tocobaga* new genus (Bulimulidae) on the basis of a distinctive suite of morphological characters, particularly those of the peristome and the embryonic whorl sculpture. Examination of all type material of the fossil taxa historically assigned to *Hyperaulax* reveals that only three species are separable (*Partula americana* Heilprin, 1886; *Bulimulus americanus wakullae* Mansfield, 1937; and *Bulimulus floridanus* Conrad, 1846). The varietal names *Bulimulus americanus* var. *partulinus* and *B. americanus* var. *laxus*, both Dall, 1890, are indistinguishable from the nominate form in any important morphological character. *Bulimulus heilprinianus*, *Bulimulus stearnsii*, both Dall, 1890, and *Bulimulus ballistae*, *Bulimulus remolina*, *Bulimulus tampae*, and *Bulimulus tortilla*, all Dall, 1915, are synonyms of *B. floridanus* Conrad, 1846. The status of *B. a. wakullae* from northern Florida is problematic. Although clearly not conspecific with *P. americana*, it is tentatively assigned to *Tocobaga* new genus and is herein elevated to species level. The biogeography of *Tocobaga* new genus is tentatively discussed. Fossiliferous deposits in North America and South America have not yielded taxa with the combination of shell characters found in the new genus and relationships with other bulimulid genera are unknown. However, it is probable that the new genus, like other non-marine mollusks from the Tampa Member of the Arcadia Formation, dispersed to Florida after contact between the Caribbean Plate and the Bahama Platform (circa 38 Ma).

*Additional Keywords:* *Tocobaga* new genus, Miocene, Florida

## INTRODUCTION

*Hyperaulax* Pilsbry, 1897a (type species, *Bulimulus ridleyi* E. A. Smith, 1890) was described as a subgenus of *Bulimulus* Leach, 1814 (Bulimulidae Tryon, 1867) to encompass taxa having axial wrinkles on the embryonic whorls and a distinct channel at the posterior insertion of the outer lip. Pilsbry (1901: 102–103) elevated *Hyperaulax* to genus level with the “section” *Bonnanius* Jousseaume, 1900 and transferred it to the then subfamily Odontostominae, but did not alter the composition of the taxon, which consisted of the extant *H. ridleyi* and *H. ramagei* (both E.A. Smith, 1890) from Fernando Noronha Island, Brazil and several upper Tampa Member (Arcadia Formation) species from the Ballast Point site in Florida. Another fossil species from the western United States, *Bulimulus limnaeiformis* Meek and Hayden, 1856 was tentatively transferred to *Hyperaulax* by Wenz (1923: 731), but is now assigned to the Viviparidae (see Henderson, 1935 for references). *Bonnanius* Jousseaume, 1900 is currently treated as a distinct genus (Simone, 2006; Breure and Ablett, 2012), type species *B. ramagei*, thus restricting *Hyperaulax* to its type species *H. ridleyi* and the Florida fossil species. The basis for the assignment of the fossil species to *Hyperaulax* was the striking similarity in shell shape, size, and peristome characters between the fossil taxa and the extant *H. ridleyi* and, in particular, the presence in all taxa of a narrow channel at the junction of the outer lip with the body whorl (Pilsbry, 1897b: 82; 1901: 102–103).

Recently, we examined numerous specimens of Ballast Point bulimulids housed in the Invertebrate Paleontology Collection at the Florida Museum of Natural History (FLMNH) and all type material of Florida fossil taxa assigned to *Hyperaulax*. We concluded that several unnecessary names had been introduced for the Florida fossils. By comparing these fossil specimens to *Hyperaulax ridleyi* and the type species of all other pertinent bulimulid genera and subgenera, we find that the placement of the

<sup>1</sup> Corresponding author

early Miocene fossils is best resolved by formally recognizing their distinctive suite of characters with a new generic epithet. We therefore adopt the name:

#### SYSTEMATIC PALEONTOLOGY

##### *Tocobaga* new genus

**Diagnosis:** Shell ovate to ovate-cylindrical in shape. Whorls 5.5–6; embryonic whorls approximately 1.2–1.3, bluntly rounded and spirally striate; later whorls sculptured with weak to moderately strong axial riblets, spiral incised lines often present in interspaces, occasionally crossing axial riblets; last half of body whorl slightly flattened behind peristome, ascending for last 0.2 whorl; sutures shallow to well-impressed. Peristome broadly expanded and thickened internally, often strongly thickened basally; inner and outer margins connected by distinct parietal callus, interrupted by narrow channel at posterior insertion of outer lip; marginal palatal tooth robust, weak or lacking when prominent, forming distinct sinus at upper insertion of outer lip, buttressed below. Aperture ovate to subquadrate in shape. Columella simple, lacking lamellae. Umbilicus narrow, chink-like.

**Type Species:** *Partula americanana* Heilprin, 1886, Ballast Point, Hillsborough Bay, Hillsborough County, Florida, upper Tampa Member, Arcadia Formation (early Miocene).

**Content:** *Tocobaga americanus* (Heilprin, 1886), *T. floridanus* (Conrad, 1846), and *T. wakullae* (Mansfield, 1937).

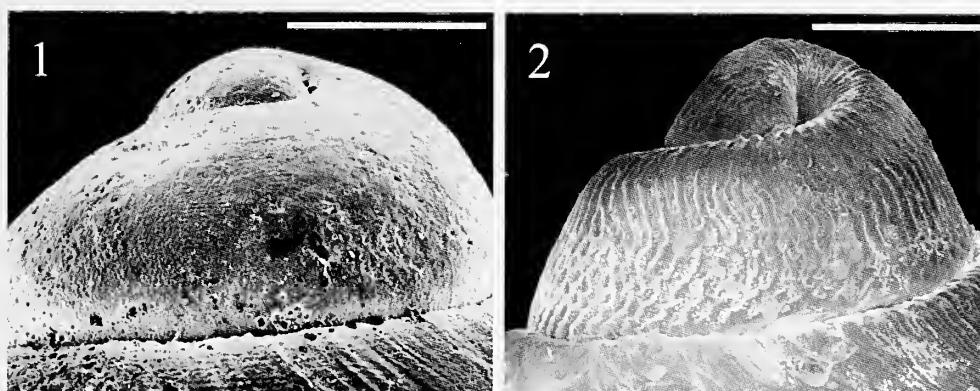
**Etymology:** The name *Tocobaga* is derived from the Tocobaga Tribe of Native Americans that, like these extinct snails, inhabited the Tampa Bay region, albeit 23 million years later. Tocobaga was first used in Spanish documents of the 1560s in reference to the male chief of the group, the chief's village, as well as the people themselves. Since no gender was implied when the

name was established, we treat the genus name *Tocobaga* as masculine.

**Discussion:** The primary shell character used to differentiate many genera of Orthalicoidea Albers, 1860 is the embryonic whorl sculpture (Pilsbry, 1895, 1896). The efficacy of this character is supported at least in part by independent genetic evidence (Breure and Romero, 2012). The embryonic whorl sculpture of *Tocobaga americanus* is microscopically spirally striate (Figure 1) while that of *Hyperaulax ridleyi*, the type species of that genus, is axially wrinkled (Figure 2). This character alone serves to remove the fossil species from *Hyperaulax*. In addition, the first embryonic whorl of the Florida fossils is low, rounded with a weakly impressed suture (Figure 1), while that of *H. ridleyi* is greatly elevated, with a deeply channelled suture (Figure 2). These features of the embryonic whorl clearly indicate that the fossil taxa have been erroneously assigned to *Hyperaulax*.

The early assignment of these species to the orthalicoid family Bulimulidae was logical given their close resemblance in gross shell morphology to several extant bulimulid taxa and the biogeography of the Caribbean Basin. The only families outside the orthalicoids that serve as reasonable alternatives to this arrangement on the basis of shell morphology are the Partulidae and Enidae. In fact, Heilprin (1886) described *T. americanus* as a species of *Partula* Férrussac, 1821, and Moellendorff (1901) suggested that *H. ridleyi* belonged to the enid genus *Napaeus* Albers, 1850. Hence, the evidence for the placement of the fossil taxa in the Bulimulidae is examined below.

The fossil species are readily distinguished from partulids by a variety of features. Of greatest importance are features of the embryonic whorls. Both partulids and *Tocobaga* have spirally striate embryonic whorls, but the striae of the partulids are much coarser. The embryonic whorls of partulids are conic and flat-sided, with barely any relief at the suture; the embryonic whorls of *Tocobaga* are rounded at the periphery, more globose, and with more distinct sutures. The later whorls of partulids are more rapidly expanding than those of *Tocobaga* and the



**Figures 1–2.** Embryonic whorl sculpture of *Tocobaga* new genus and *Hyperaulax*. 1. *Tocobaga americanus* (Heilprin, 1886). UF 66651 (Invertebrate Paleontology Collection). 2. *Hyperaulax ridleyi* (E.A. Smith, 1890). UF 109915 (Malacology Collection). Scale bar = 0.5 mm.

shells typically have an incomplete peristome lacking the parietal callus and associated groove at the junction of the outer lip with the body whorl that characterizes *Tocobaga*. From these characters it can readily be seen that the relationship of the early Miocene fossils is not with the partulids.

Separating *Tocobaga* from the Enidae on the basis of shell morphology is more difficult. Many enid taxa have shell morphologies very similar to that of *Tocobaga* (i.e., a channel at the posterior insertion of the outer lip and an expanded peristome). Enid embryonic whorls may be smooth or spirally striate. The fossil genus *Dendropupa* Owen, 1859 (see below), has axial sculpture on the embryonic whorls (Solem and Yochelson, 1979). The enid body whorl may ascend behind the peristome, but does not become flattened near the aperture as in *Tocobaga*. The primary reason for excluding *Tocobaga* from assignment in the Enidae is biogeographic. The enids are currently restricted to Europe, northern Africa, central and southern Asia, and the Pacific from Indonesia to Melanesia. Known fossils of this family are restricted to the same locations with the exception of *Dendropupa*, which has been collected from Upper Carboniferous sediments in eastern Canada, France, and Poland (Solem and Yochelson, 1979). Other enid fossils are known from the Paleocene of Europe and later records through the Tertiary of Europe, Africa, and the Middle East through Central Asia to China (Zilch, 1959). Solem and Yochelson's assignment indicates a possible Laurasian origin for the Enidae and a distribution of *Dendropupa* that pre-dates the separation of North America and Europe. However, the Enidae is unknown in subsequent North American land snail faunas and there is no other evidence that it constituted a component of the American Miocene fauna. Thus, we agree with Pilsbry (1901) that the resemblance of *Hyperaulax* and the Florida fossils to certain members of the Enidae is most likely the result of convergent adaptations to dry habitats. The thickened peristome allows for an efficient shell/substrate seal during aestivation, while the canal acts as a contact to the exterior.

The current geographic distribution of Orthalicoidea including the Bulimulidae strongly suggests that bulimulids could be expected in the fossil fauna of the Caribbean Basin, including early insular environments on the Florida Platform. Among Orthalicoidea families, *Tocobaga* is best assigned to the Bulimulidae. It is readily separated from the Amphibulimidae P. Fischer, 1873 (e.g., *Amphibulima* de Montfort, 1810) on the basis of shell shape and degree of calcification. The fossils do not belong with the Orthalicidae Albers, 1860 (e.g., *Liguus* de Montfort, 1810) because those taxa have larger, imperforate shells and a simple lip. *Tocobaga* cannot be assigned to the Odontostomidae because of the elevated embryonic whorls of the latter, lacking in spiral sculpture as discussed above. In addition, most odontostomids have apertural barriers. Hence, we agree with earlier authors that the Florida fossil species are properly assigned to the Bulimulidae.

The distinctively striate embryonic whorls of *Tocobaga* differ from all other North American and Antillean Bulimulidae which are either axially ribbed as in *Bulimulus* Leach, 1814 and *Rabdotaus* Albers, 1850, or both axially and spirally ribbed as in *Drymaeus* Albers, 1850. Dall (1890) tentatively assigned all Florida taxa known at that time to the South American group *Anctus* Martens, 1860, based on similarities such as a laterally compressed body whorl behind a broadly reflected peristome. However, the embryonic whorls of *Anctus* are smooth and lack the channeled and calloused parietal area. Only the South American genera, *Lopesianus* Weyrauch, 1958, *Leiostracus* Albers, 1850, *Discoleus* Breure, 1978, and some *Bostryx* sensu lato Troschel, 1847 possess a similarly striate embryonic whorl sculpture. Of these genera, *Lopesianus* differs from *Tocobaga* in having fewer and stronger spiral striae on the embryonic whorls (Weyrauch, 1958: pl. 6, figs. 8); deeply channeled, crenulate sutures; no parietal callus; and an incomplete, simple peristome. *Leiostracus* differs in having the spiral striae confined to the lower half of each whorl; papilliform embryonic whorls; and an incomplete peristome only slightly expanded. *Discoleus* differs in having a larger, more bulbous embryonic whorl; a subovate aperture; more convex whorls; and a simple, incomplete peristome.

The polyphyletic genus *Bostryx* sensu lato (Breure and Romero, 2012) is the most difficult genus from which to distinguish *Tocobaga*, a reflection of the presumably diverse nature of the former. In each of several characters, one or a few species of *Bostryx* sensu lato can be found that approach the state seen in *Tocobaga*. However, in no case does any species of *Bostryx* sensu lato approach the entire suite of characters that serve to distinguish the fossils from other Bulimulidae.

We examined the type species of all but two (*Elatibostryx* Weyrauch, 1958 and *Kionoptyx* Haas, 1966) of the 21 generic synonyms (or subgenera) given by Breure (1979) as belonging to *Bostryx* sensu lato to determine whether any of these names could apply to the early Miocene fossils. All but *Peronaeus* Albers, 1850, *Platybostryx* Pilsbry, 1896, *Phenacotaxus* Dall, 1912, *Scansicohlea* Pilsbry, 1930, and *Pampasinus* Weyrauch, 1958 can be dismissed for having embryonic whorls that are entirely smooth or having a combination of spiral and axial sculpture (the type of *Bostryx* sensu stricto, *B. solutus* (Troschel, 1847) has smooth embryonic whorls). *Elatibostryx* and *Kionoptyx* are disregarded because of their dissimilar embryonic whorl sculpture and/or shell morphology mentioned in the original descriptions (Haas, 1966: 239; Weyrauch, 1958: 113). *Peronaeus*, *Pampasinus*, and *Platybostryx* can be eliminated on the basis of shell shape. The first is greatly elongated, and the other two genera are thick and lens-shaped. *Phenacotaxus*, *Scansicohlea*, and *Tocobaga* have similar shell shapes, but do not agree in any other of the characters we use to distinguish the latter. *Phenacotaxus* and *Scansicohlea* have simple peristomes, their body whorls do not ascend near the aperture and are evenly expanded, not flattened behind the

**Table 1.** Shell morphometrics of type specimens of nominate forms of *Tocobaga*. L = shell length, W = shell width, ApL = aperture length, ApW = aperture width; all measurements in mm, X = no measurement possible. Bold species are considered valid.

vouchers	taxon	L	W	L/W	ApL	ApW	ApL/ApW	no. of whorls	Complete
WFIS 865	<b><i>americanus</i></b>	15.9	8.4	1.9	8.2	4.9	1.7	6+	Yes
USNM 111971	<i>laxus</i>	15.1	8.1	1.9	7.2	4.8	1.5	6.5±	Yes
USNM 111970	<i>partulinus</i>	15.1	8.0	1.9	8.0	5.0	1.6	6±	No
ANSF 30607	<b><i>floridanus</i></b>	9.4	4.0	2.4	4.6	2.8	1.6	4±	No
USNM 165013	<i>ballistae</i>	8.6	4.2	2.1	3.2	2.0	1.6	5±	No
USNM 111962	<i>heilprinianus</i>	10.2	4.7	2.2	3.4	2.2	1.6	6±	No
USNM 165014	<i>remolina</i>	9.5	4.3	2.2	3.8	2.2	1.7	6±	No
USNM 111964	<i>stearnsii</i>	13.5	5.9	2.3	4.5	2.5	1.8	4±	No
USNM 165012	<i>tampae</i>	13.5	6.1	2.2	4.5	2.8	1.6	6.6	Yes
USNM 165015	<i>tortilla</i>	10.8	4.9	2.2	3.3	2.0	1.7	5±	No
USNM 495932	<b><i>wakullae</i></b>	26.5	X	X	14.1±	X	X	6±	No

peristome. It is clear that the morphology of *Tocobaga* is unique, that this taxon has no close resemblance to any of the name-bearing species currently synonomized with *Bostryx* sensu lato, and that consequently, none of these names can serve to accommodate the Florida fossils.

Examination of the holotypes of all named fossil “*Hyperaulax*” indicates that only three species are recognizable in the Florida fossils; the taxa described by Dall (1890, 1915) are synonyms of either *T. americanus* or *T. floridanus*. Below we diagnose and discuss each species. Shell length, shell width, aperture length, and aperture width (Tables 1–2) were measured as described in Crampton (1916) for similarly shaped *Partula*. We use the following institutional abbreviations: ANSP

(Academy of Natural Sciences of Drexel University), UF (Florida Museum of Natural History, University of Florida), USNM (National Museum of Natural History, Smithsonian Institution), and WFIS (Wagner Free Institute of Science, Philadelphia).

## SYSTEMATICS

### *Tocobaga americanus* (Heilprin, 1886) new combination

(Figures 3–7, Tables 1 and 2)

*Partula americana* Heilprin, 1886: 115, pl. 16, fig. 60.

*Bulimulus* (? *Anctus*) *americanus* var. *partulinus* Dall, 1890: 7; 1915: 26, pl. 4, fig. 12.

*Bulimulus* (? *Anctus*) *americanus* var. *laxus* Dall, 1890: 7; 1915: 26, pl. 4, fig. 14.

*Bulimulus* (*Hyperaulax*) *patulinus* Mansfield, 1937: 24–25 (*lapsus calami*)

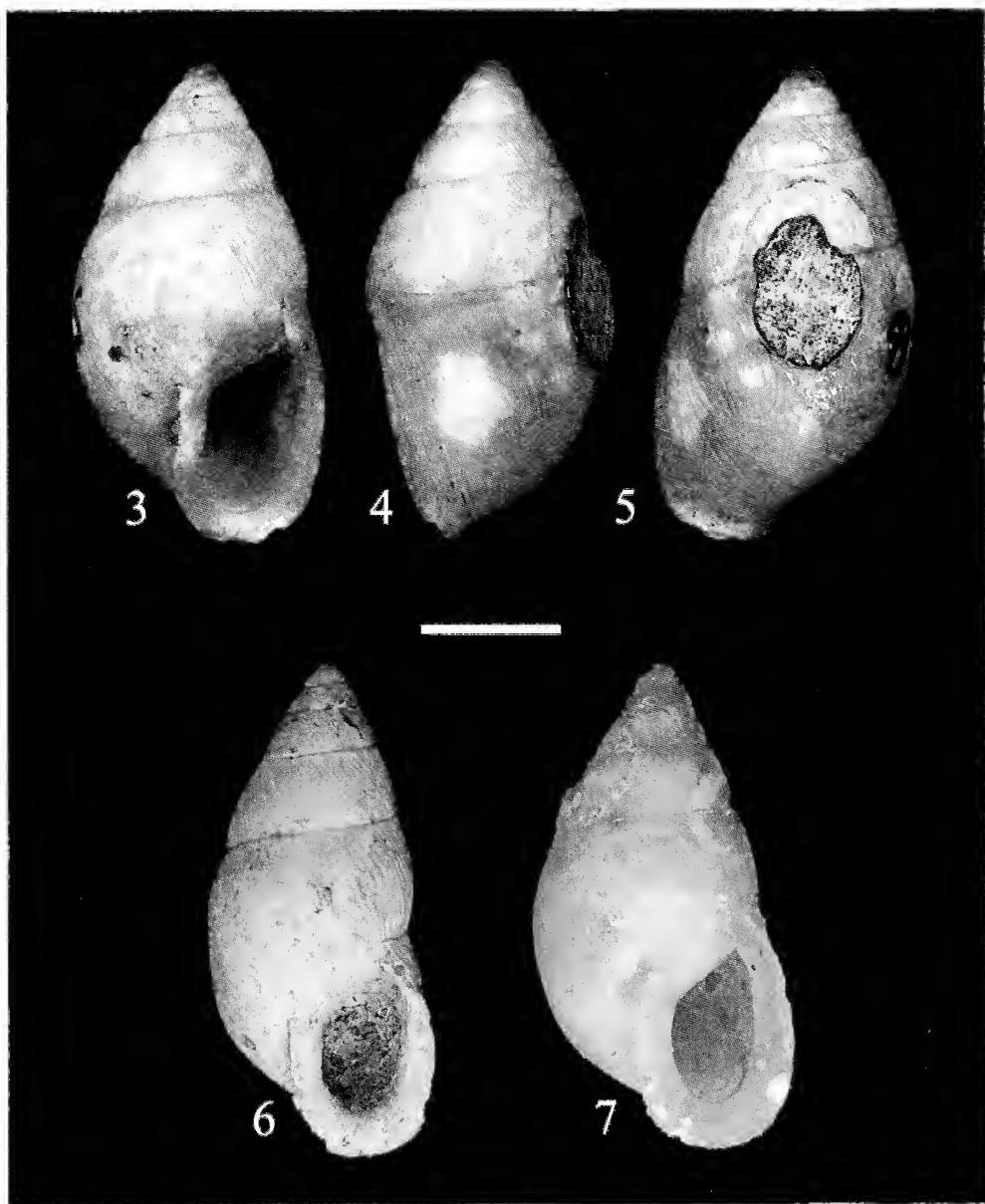
**Diagnosis:** A large species of *Tocobaga*, 15–17 mm in height, 6–8 mm in width; shell ovate in shape; whorls approximately 5.5–6.5, slightly convex; shell sculpture of evenly spaced oblique riblets of width equal to their inter-spaces; last half of body whorl slightly flattened, ascending for last 0.2 whorl; aperture subquadrate; peristome with a wide, flat expansion, thickened internally throughout, almost complete, inner and outer margins connected by a thickened parietal callus; a narrow channel present at posterior insertion of outer lip, parallel to the long shell axis; umbilicus narrow; columella simple and straight.

**Holotype:** WFIS 865 (Figures 3–5) Ballast Point, Hillsboro [Hillsborough] Bay, [Tampa, Hillsborough County], Florida, upper Tampa Member, Arcadia Formation (early Miocene). J. Willcox and A. Heilprin, 1886.

**Remarks:** *Tocobaga americanus* is readily distinguished from *T. floridanus* by its larger size and more ovate shape; more rapidly expanding whorls; peristome that is expanded along the entire outer margin; channel at

**Table 2.** *Tocobaga americanus* (Heilprin, 1886) shell morphometrics; L = shell length, W = shell width, ApL = aperture length, ApW = aperture width; number of whorls of all measured fossils estimated at 6+ due to erosion of embryonic whorls. All measurements in mm.

Cat. No.	L	W	L/W	ApL	ApW	ApL/ApW
UF 66653a	15.6	7.7	2.03	7.1	4.8	1.48
UF 66653b	16.3	8.1	2.01	8.3	4.8	1.73
UF 66653c	14.5	7.5	1.93	7.8	4.5	1.73
UF 66653d	14.4	7.3	1.97	7.1	4.0	1.78
UF 66653e	16.3	7.5	2.17	7.8	4.9	1.59
UF 66653f	15.9	7.7	2.06	8.1	5.0	1.62
UF 66653g	15.5	8.0	1.94	8.3	4.8	1.73
UF 66653h	16.3	8.2	1.99	8.1	5.0	1.62
UF 66653i	15.7	7.9	1.99	7.9	4.3	1.84
UF 66653j	14.8	7.2	2.06	7.2	5.0	1.44
UF 66653k	14.4	7.9	1.82	7.8	4.9	1.59
UF 66653l	17.7	8.3	2.13	8.7	4.7	1.85
UF 66653m	15.8	8.3	1.90	8.4	4.8	1.75
UF 66653n	17.3	8.3	2.08	8.0	5.5	1.46
UF 66652	17.1	8.5	2.01	8.6	5.1	1.69
UF 66651	16.3	7.8	2.09	8.4	4.5	1.87
Mean	15.9	7.9	2.01	8.0	4.8	1.67
SD	1.01	0.39	0.09	0.50	0.35	0.14



**Figures 3-7.** *Tocobaga americanus* (Heilprin, 1886). 3-5. Holotype of *Partula americana* Heilprin, 1886. WFIS 865. 6. Holotype of *Bulimulus americanus* var. *laxus* Dall, 1890. USNM 111971. 7. Holotype of *Bulimulus americanus* var. *partulinus* Dall, 1890. USNM 111970. Scale bar = 5 mm.

the posterior insertion of the outer lip that is parallel to the main axis of the shell; and a more open umbilicus.

The holotypes of Dall's (1890) varieties *laxus* (Figure 6) and *partulinus* (Figure 7) are indistinguishable from typical *T. americanus* in any important detail. The shells of *laxus* are more slender and have stronger axial sculpture, while those of *partulinus* are even more slender. However, both are also shorter in length than typical *T. americanus* and all three have identical length to width ratios. Similarly, the length to width ratios of the aperture is also alike (Table 1). Variation among 16 unbroken individuals of 59 specimens in UF lots 66651, 66652, and 66653 (Table 2) include a morphological range in

shell length and width and apertural length and width that encompasses the two varietal names and we see no need to recognize this natural variation with formal epithets. Specimens from Wakulla County, Florida questionably referred to these forms (Mansfield, 1937) were not located.

**Material Examined:** *Partula americana* Heilprin, 1886, Holotype, WFIS 865; *Tocobaga americanus* (Heilprin, 1886), UF 66651 (1), UF 66653 (57), USNM 111965 (1); *Bulimulus americanus* var. *partulinus* Dall, 1890, Holotype, USNM 111970; *Bulimulus americanus* var. *laxus* Dall, 1890, Holotype, USNM 111971.

***Tocobaga floridanus* (Conrad, 1846) new combination**  
(Figures 8–16, Table 1)

*Bulimus floridanus* Conrad, 1846: 399, text-figure.  
*Bulimus (Bulimulus) longaevis* Ancey, 1881: 414.  
*Bulimulus* (? *Anctus*) *heilprinianus* Dall, 1890: 6–7, pl. 1, figs. 6b, 10.  
*Bulimulus* (? *Anctus*) *stearnsii* Dall, 1890: 7–8, pl. 1, fig. 12.  
*Bulimulus* (*Hyperaulax*) *ballistae* Dall, 1915: 26–27, pl. 1, fig. 5.  
*Bulimulus* (*Hyperaulax*) *remolina* Dall, 1915: 27–28, pl. 1, fig. 18.  
*Bulimulus* (*Hyperaulax*) *tampae* Dall, 1915: 26, pl. 1, fig. 3.  
*Bulimulus* (*Hyperaulax*) *tortilla* Dall, 1915: 27, pl. 1, fig. 2.

**Diagnosis:** A smaller species of *Tocobaga*, 8.1–14.1 mm in height, 3.6–6.0 mm in width; shell ovate to ovate cylindrical in shape; whorls 5–6.5, slightly convex to flattened; embryonic whorl blunt, rounded, sculpture unknown; shell sculpture of evenly spaced oblique riblets of width equal to their interspaces, weak spiral incised

lines occasionally present in interspaces; body whorl not evenly expanded, last half whorl slightly flattened, ascending last 0.2 whorl; aperture oval to subquadrate; peristome expanded, thickened on inner margin along the columellar area, basally and along anterior half of outer lip; inner and outer peristome connected by a parietal callus; narrow channel present at posterior insertion of outer lip that is deflected medially at 45° relative to shell long axis; umbilicus very narrow, chink-like; columella simple and straight.

**Holotype:** ANSP 30607 (Figures 8–10). Nine miles from Tampa on Hillsboro [Hillsborough] River, [Hillsborough County], Florida, upper Tampa Member, Arcadia Formation (early Miocene). The holotype is a broken specimen. The inadequate original text-figure apparently depicts a reconstruction.

**Remarks:** *Bulimulus longaevis* Ancey, 1881 is an unnecessary replacement name for *Bulimus floridanus* Conrad, 1846 (see Henderson, 1935), not *B. floridanus* Pfeiffer,



**Figures 8–16.** *Tocobaga floridanus* (Conrad, 1846). **8–10.** Holotype of *Bulimus floridanus* Conrad, 1846. ANSP 30607. **11.** Holotype of *Bulimulus ballistae* Dall, 1915. USNM 165013. **12.** Holotype of *Bulimulus heilprinianus* Dall, 1890. USNM 111962. **13.** Holotype of *Bulimulus remolina* Dall, 1915. USNM 165014. **14.** Holotype of *Bulimulus stearnsii* Dall, 1890. USNM 111964. **15.** Holotype of *Bulimulus tampae* Dall, 1915. USNM 165012. **16.** Holotype of *Bulimulus tortilla* Dall, 1915. USNM 165015. Scale bar = 5 mm.

1857, as demonstrated by Wood and Gallichan (2008: 60). Ancey (1881: 414) erroneously stated that *B. floridanus* Pfeiffer, 1857 was described prior to Conrad's taxon (1846), leading Wood and Gallichan (2008) to misinterpret Ancey's intent. The holotypes of Dall's species *Bulimulus ballistae*, *B. heilprinianus*, *B. remolina*, *B. stearnsii*, *B. tampae*, and *B. tortilla* while differing in size are all similar in shape (Figures 8–16) and shell length to width and aperture length to width ratios both to each other and to the holotype of *Bulimus floridanus* (Table 1). The holotype of *Bulimulus ballistae* (Figure 11) is nothing more than a rather small specimen of *Tocobaga floridanus* differing from that species in no obvious detail. The holotypes of *Bulinulus heilprinianus* (Figure 12) and *Bulinulus tortilla* (Figure 16) differ from the typical *T. floridanus* only in having a more pronounced thickening on the anterior half of the inner margin of the outer lip. The holotype of *B. floridanus* is not fully mature and so does not prominently exhibit this character. The holotype of *Bulinulus tampae* (Figure 15) is merely a large specimen of *T. floridanus* and differs in no characters other than its size. The holotype of *Bulinulus remolina* (Figure 13) is slightly more elongate than typical *T. floridanus* and has a rather flattened body whorl with the sculpture largely eroded. The holotype of *Bulinulus stearnsii* (Figure 14) is the most unusual specimen examined. This specimen is quite elongate and large; with narrow, flattened whorls; almost lacking in shell sculpture. We believe the smooth surface is due to erosion, because traces of the characteristic ribbing of *Tocobaga* remain on a few surfaces, most prominently behind the aperture. The specimen's large size and elongate shape appear to represent one extreme of the variation in *T. floridanus*. The holotype

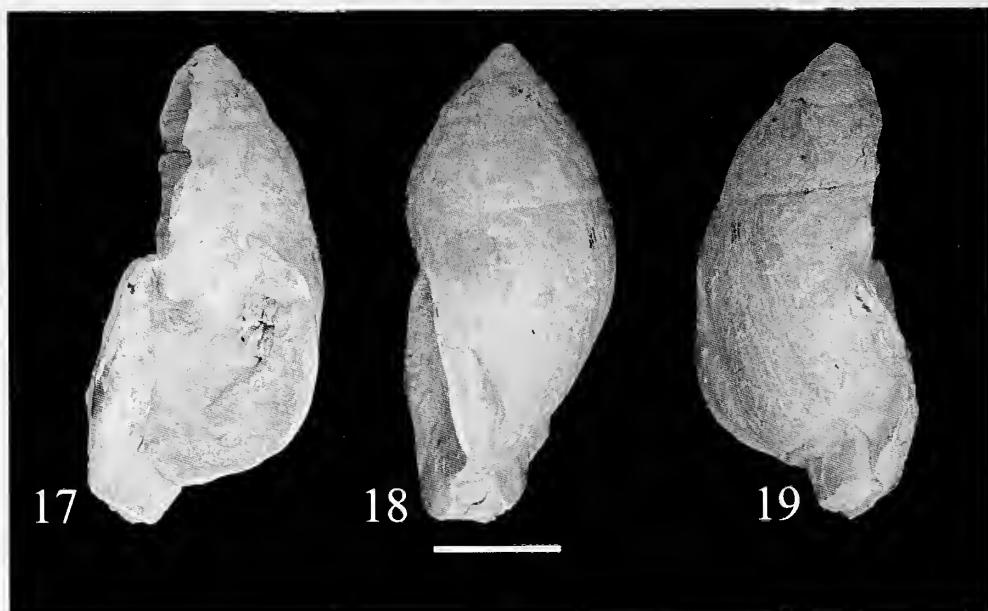
of *B. remolina* and other specimens (USNM 646161) are intermediate in shape between the holotype of *B. floridanus* and that of *B. stearnsii*, or are equally as flattened as the type of *B. stearnsii*, although not as large. The extreme elongation in the holotype of *B. stearnsii* is partly, but not entirely, a reflection of its large size, though other large specimens of *T. floridanus* (e.g., USNM 646160) are more ovate in shape. Given the continuum in size and shape that occurs between the holotypes of *B. floridanus* and *B. stearnsii*, and the apparently eroded nature of the latter's smooth surface, we believe the holotype of *B. stearnsii* represents one extreme of the morphological variation seen within *T. floridanus*.

**Material Examined:** *Bulimus floridanus* Conrad, 1846, holotype, ANSP 30607; *Tocobaga floridanus* (Conrad, 1846), USNM 111960 (1), USNM 111961 (7) USNM 646160 (5), USNM 646161 (5), USNM 646162 (1); *Bulinulus heilprinianus* Dall, 1890, holotype, USNM 111962; *Bulinulus stearnsii* Dall, 1890, holotype, USNM 111964; *Bulinulus tampae* Dall, 1915, USNM 165012; *Bulinulus ballistae* Dall, 1915, holotype, USNM 165013; *Bulinulus remolina* Dall, 1915, holotype, USNM 165014; *Bulinulus tortilla* Dall, 1915, holotype, USNM 165015.

***Tocobaga wakullae* (Mansfield, 1937) new combination** (Figures 17–19, Table 1)

*Bulinulus americanus wakullae* Mansfield, 1937: 15:70, pl. 1, figs. 10, 13.

**Diagnosis:** A large species of *Tocobaga*, ca. 26 mm in height, >10 mm in width; shell ovate in shape; whorls approximately 6.5, slightly convex; embryonic whorl blunt, rounded, sculpture unknown; later whorl sculpture of



**Figures 17–19.** *Tocobaga wakullae* (Mansfield, 1937). Holotype of *Bulinulus americanus wakullae* Mansfield, 1937. USNM 495932. Scale bar = 5 mm.

evenly spaced axial riblets more or less parallel to shell long axis, spiral sculpture not apparent; body whorl very slightly flattened behind apertural lip, ascending very slightly for last 0.2 whorl; aperture ovate, slightly oblique; peristome moderately reflected, but not greatly expanded or thickened within; parietal area with weak callus; channel at posterior insertion of outer lip not apparent; characters of umbilical area unknown; columella simple, unadorned.

**Holotype:** USNM 495932 (Figures 17–19). About 200 yards south of Wakulla Railroad Station, Wakulla County, Florida. External mold and cast.

**Remarks:** Mansfield (1937) originally placed this taxon as a subspecies of *Tocobaga americanus*, but it differs from that species in its larger shell size, in having an ovate instead of subquadrate aperture, in its more inflated shape, and in having the axial shell sculpture oriented more nearly parallel to the long axis of the shell. These differences in shell characters lead us to conclude that these two taxa are separate species.

Our assignment of this taxon in *Tocobaga*, however, is not without reservation. Several of the diagnostic features of that genus, such as the embryonic whorl sculpture, the channel at the posterior insertion of the outer lip, and the nearly complete peristome, cannot be examined in the holotype of *B. wakullae* (the only specimen available to us) because of its poor preservation (an external mold) and casting material. Collection of additional material may allow assessment of these particular characters, whereby the generic allocation of *B. wakullae* may well be revised.

*Tocobaga wakullae* (Mansfield, 1937) was described from the “Tampa Limestone” of Wakulla County in northwestern Florida. Although Mansfield (1937) did not discuss the stratigraphy of the type locality, the type specimen was probably collected from what is now considered the St. Marks Formation. This formation is early Miocene in age (Rupert and Spencer, 1988) and approximately contemporaneous with the upper Tampa Member (Arcadia Formation) of the Tampa Bay area.

**Material Examined:** *Bulimulus americanus wakullae* Mansfield, 1937, Holotype, USNM 495932, external mold and cast.

## BIOGEOGRAPHY

Modern orthalicoids are particularly diverse in South America with a few lineages in Africa, Australia, Melanesia, and New Zealand. The group appears to have a Gondwanan distribution (Herbert and Mitchell, 2009). However, the family is well represented in Mexico, Central America, and the Antilles and there are representatives of a few genera in temperate North America including the bulimulids *Drymaeus* and *Rabdotus*. Several other Antillean land snail groups were widely distributed in North America during the late Cretaceous and early Tertiary (Bishop, 1979;

Roth and Hartmann, 1998) and became restricted to the Antilles as climate cooled in the Tertiary. However, the oldest North American fossil bulimulids are the Florida Miocene fossils reviewed here and there is yet no evidence that bulimulids were present in North America before then. The oldest bulimulids are from a middle Paleocene site in southern Brazil where the family accounts for more than 30% of fossil species diversity (Salvador and Simone, 2013). The family remains the most diverse family in South America accounting for approximately 45% of recent South American species (Simone, 2006).

Many of the Florida Tampa Member (Arcadia Formation) land snails are similar in shell morphology to extant Antillean species (Pilsbry, 1897a; Auffenberg and Portell, 1990). Fossil species were assigned to the extant Antillean genera *Plagiptycha* Pfeiffer, 1855, *Cepolis* de Montfort, 1810, and *Pleurodonte* Fischer de Waldheim, 1807, *Gongylostoma* Albers, 1850, and *Cerion* Röding, 1798 (Dall, 1915; Mansfield, 1837). While the placement of these fossil taxa in modern genera can be questioned, the fauna surely has a degree of Caribbean affinity. The Antillean component of the Tampa Member (24–22.5 Ma, but see Scott, 1988) species apparently dispersed over water to Florida after contact between the Caribbean Plate and the Bahama Platform 38 Ma (Duncan and Hargraves, 1984). Reexamination of the entire fauna may provide a better understanding of its biogeography.

Relationships between *Tocobaga* and recent bulimulid genera remain unknown. Fossiliferous deposits in North America have not yielded taxa closely similar to *Tocobaga* and the extinct South American fossil genera, *Paleobulimulus* Parodiz, 1949 and *Itaborahia* Maury, 1935, have shell morphologies quite unlike *Tocobaga* (Parodiz, 1969).

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# First report of the Eocene gastropod *Mitrella (Bastropia)* (Neogastropoda: Columbellidae) from the northeast Pacific and paleobiogeographic implications

Richard L. Squires

Department of Geological Sciences  
California State University  
Northridge, CA 91330–8266 USA  
and

Invertebrate Paleontology<sup>1</sup>  
Natural History Museum of Los Angeles County  
Los Angeles, CA 90007 USA  
richard.squires@csun.edu

## ABSTRACT

The columbellid neogastropod *Mitrella (Bastropia) llajasensis* new species is described from a lower Eocene siltstone bed in the shallow-marine part of the Llajas Formation, Ventura County, southern California. This new species, which lived in a warm-water environment, is the first record of *Bastropia* Palmer, 1937 in the northeast Pacific region. *Bastropia* differs from *Mitrella* Risso, 1826 by having axial riblets on an early part of the spire and a longer and more constricted anterior canal. In addition, the majority of species of *Bastropia* have incised-spiral line(s), with or without pits, near the suture on the posterior part of the lower spire whorls and on the last whorl. The geologic range of *Bastropia* is late Paleocene? (Thanetian?) and early Eocene (Ypresian) to late middle Eocene (Bartonian). Its previous occurrences are in Alabama (oldest occurrence), Texas, and South Island, New Zealand (youngest occurrence). *Bastropia* most likely had planktotrophic larval development, and the introduction of *Bastropia* into California from the Gulf Coast region was closely associated with the “Early Eocene Climatic Optimum” (EECO), a time of global warmth and high sea level.

*Additional Keywords:* Simi Valley, thermophilic

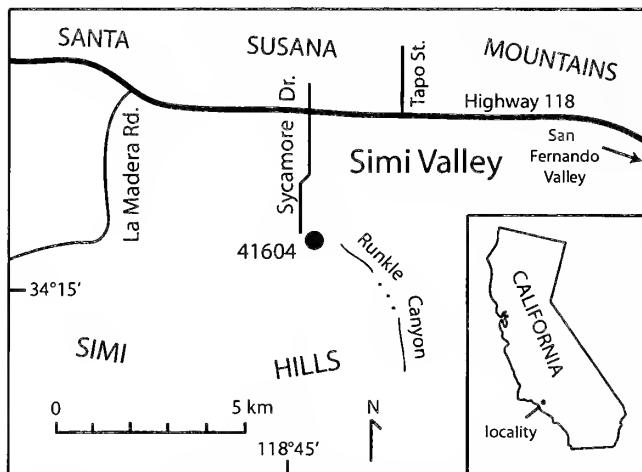
## INTRODUCTION

Neogastropods first became abundant during the Early Cretaceous (late Albian) (Kiel, 2002) and subsequently became increasingly diversified. One of the post-Cretaceous neogastropod groups is family Columbellidae Swainson, 1840. According to Schnetler (2001), the earliest known columbellids are of Paleocene age, belong to *Astyris*

H. and A. Adams, 1853, and are found in northern Europe and Greenland. The global Paleogene (Paleocene to Oligocene) record of columbellids is meager. In the northeast Pacific, in a region extending from southwestern Washington to southern California, their record is extremely rare. The only Paleogene columbellid reported previously from this particular region is *Mitrella (Mitrella) blackhillsensis* (Squires and Goedert, 1994), of middle early Eocene age from the Crescent Formation in southwestern Washington. This present study concerns the columbellid *Mitrella (Bastropia) llajasensis* new species of late early Eocene age from the Llajas Formation in southern California (Figure 1). *Bastropia* Palmer, 1937 is known previously from Eocene strata in Alabama, Texas, and South Island, New Zealand (Table 1).

Columbellids underwent great diversification during the Miocene to Holocene. For example, a great array of columbellids is found in middle Miocene deposits of the Caribbean region (Woodring, 1964: 246). Today, columbellids comprise a highly diverse group with about 400 extant species. Their shells are small, normally between 3 and 20 mm in height. Most columbellids are active epibenthic carnivores or scavengers, but some feed on algae. Herbivory is uncommon among neogastropods, and only the columbellids and nassariine buccinids include herbivorous species. Columbellids today have worldwide distribution, mainly in tropical and warm-temperate seas, but a few species inhabit high-latitude and deep-ocean environments (deMantenon, 1999: 2008). Columbellids have larval-developmental strategies ranging from embryos hatching into planktotrophic veliger larvae (indirect development) to embryos hatching into small crawling snails (non-pelagic development) (Bandel, 1974). Columbellids can have determinate growth, thus, at adulthood there is thickening of the outer lip, with concomitant development of denticles

<sup>1</sup> Research Associate



**Figure 1.** Index map of LACMIP locality 41604, the type locality of the new species.

on the interior surface of the outer lip (deMantenon, 2005: 501; Pernet, 2007).

## MATERIALS AND METHODS

The new species is based on a well-preserved single specimen. Its small size (8 mm height) is most likely why this species has been previously overlooked. Shells of this size are commonly firmly cemented in rock matrix in the Llajas Formation, and, as a result, they are easily destroyed during the process of collecting. In the case of the new species, however, it was found in relatively soft matrix, which was easily removed by picking at the grains with a very sharp, small needle. The lower and middle Eocene provincial molluscan “stages” mentioned in the text are informal (in quotation marks) and, as discussed by Squires (2003), apply mainly to California. Morphologic terms are from Cox (1960). Supergeneric classification is based on Bouchet and Rocroi (2005: 254).

## STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENT

Squires (1984, 2001) provided details of the stratigraphy, depositional environments, and paleontology of the Llajas Formation. The locality where the new species was found is in siltstone within the middle lower part of the “shallow-marine (transgressive) deposits” in the formation. This part of the formation is of late early

Eocene age. Co-occurring shallow-marine, warm-water species are the large benthic foraminifer *Pseudodrphragmina (Proporocyclina) clarki* (Cushman, 1920) and the goneplacid crab *Glypithyreus weaveri* (Rathbun, 1926).

## SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797

Clade Neogastropoda

Superfamily Buccinoidea Rafinesque, 1815

Family Columbellidae Swainson, 1840

**Discussion:** DeMantenon (1999, 2008) reported that columbellids have retained the basic neogastropod gut anatomy and that the herbivory observed in columbellids is probably a derived condition. The classification of columbellids is presently not well resolved, with many taxa based on morphologic groups rather than on monophyletic clades (deMantenon, 1999). Results of deMantenon’s (1999: 264) parsimony-based phylogenetic studies support a close relationship between columbellids and buccinids.

The supraspecific assignment of Paleogene columbellids has been highly unstable. The historical trend in the literature has been the usage of names belonging to extant genera. As noted by deMantenon (2008: 267), many extant and fossil species currently are placed in genus *Mitrella* Risso, 1826. DeMantenon (1999, 2008) reported, however, that *Mitrella* is not a monophyletic group, but it is a polyphyletic collective for biconic columbellids with smooth, unsculptured shells.

## Genus *Mitrella* Risso, 1826

**Type Species:** *Mitrella scripta* (Linnaeus, 1758) [= *Mitrella flaminea* Risso, 1826], by subsequent designation (see Woodring, 1928: 273); extant, Mediterranean Sea, Portugal, and Morocco (Poppe and Coto, 1991: 152).

**Description:** Shell small (approximately between 4 and 18 mm height), fusiform. Spire moderately high to high, apex subrounded to acicular-like. Protoconch low-domal, paucispiral, smooth. Teleoconch five to eight whorls. Whorls convex to flat-sided. Suture impressed to indistinct. Shell generally smooth, except for pillar (neck) area. Shell can be glossy. Axial sculpture normally absent. Those in modern taxa having rare exceptions of axial ribs on upper spire (see below) need modern systematic work and might represent different genera or subgenera.

**Table 1.** Ages and geographic distribution of *Bastropia* species.

Species	Age	Location
<i>B. subfraxa</i> (Harris, 1899)	late Thanetian?, early Ypresian	Alabama
<i>B. llajasensis</i> new species	late early Ypresian	Southern California
<i>B. bastropensis</i> (Harris, 1895)	early to middle Lutetian	Texas
<i>B. mackayi</i> (Suter, 1917)	late Lutetian to early Bartonian	South Island, New Zealand

Spiral sculpture prominent on pillar, elsewhere, minor or absent. Aperture on most species wide, short, and truncate. Columella generally straight and smooth with slight callus. Pillar commonly short. Interior of outer lip can have denticles. Area preceding outer lip can have “varix”-like swollen area.

**Discussion:** Keen (1971) reported two species of *Mitrella* that have axial riblets on the earliest teleoconch whorls. Both species are from the southern tip of Baja California, Mexico. They are *Mitrella baccata* (Gaskoin, 1852) (also see Keen, 1971: fig. 1231) and *Mitrella caulerpae* Keen (1971: fig. 1232, two views). *Mitrella baccata* has axial ribs on the first two early teleoconch whorls and has a very short anterior canal. *Mitrella caulerpae* has axial ribs on only the first teleoconch whorl, a moderately short anterior canal, and either a thick outer lip or one with a varix.

Most nominal *Mitrella*, like the extant *Mitrella pallaryi* (Dautzenberg, 1927) in the eastern Atlantic, have been reported as having planktotrophic development, inferred from the multispiral protoconch of this species (see World Register of Marine Species at <http://www.marinespecies.org>). By similar reasoning, Harzhauser and Kowalek (2002) inferred that a Miocene species of *Mitrella* had planktotrophic development. A few extant species of *Mitrella* have been observed as having nonpelagic development (Chaney and deMantenon, 2009).

### Subgenus *Bastropia* Palmer, 1937

**Type Species:** *Astyris bastropensis* Harris, 1895, by original designation, middle Eocene, Texas.

**Description:** Shell small (up to 20 mm height), slender fusiform. Spire high. Pleural angle 25° to 40°. Protoconch three smooth whorls. Teleoconch 5 to 6.5 whorls. First one to two teleoconch whorls with many and closely spaced axial riblets. Other spire whorls smooth, but posterior part of penultimate and last whorls can have incised spiral line(s), with or without many closely spaced pits. Columella straight and with slight callus. Aperture narrow and long. Anterior canal well developed and constricted. Pillar elongate and covered by many spiral ribs; those extending onto medial area of columella can create “plicate” appearance. Aperture narrow and long. Anterior canal moderately long to long, anterior canal constricted, siphonal fasciole can be distinct.

**Discussion:** The type species of *Bastropia* differs from the type species of *Mitrella* by having a narrower last whorl, axial riblets on the first and/or second teleoconch whorls, incised spiral line(s) with or without pits commonly present on posterior parts of the lower spire whorls and on the last whorl, spiral ribs present on base of the last whorl, absence of thick callus on the inner and parietal lips, thinner outer lip, and an aperture that is more distinctly constricted anteriorly. Whether or not there are denticles on the interior of the outer lip of *Bastropia* is unknown because all the specimens of the

all the species of *Bastropia* have the margin of the outer lip broken. All these specimens might be juveniles.

Palmer (1937: 282) stated that the height of the spire of *Bastropia* is greater than the height of its last whorl, but, based on measurements of the four known species of *Bastropia* listed in Table 1, this statement is incorrect. The height of the spire is actually less (in most species, slightly less) than the height of the last whorl. Modern workers have commonly identified (e.g., Palmer, 1937) or compared (e.g., MacNeil and Dockery, 1984) these four species to *Mitrella* (*Bastropia*). Maxwell (1992: 130, fig. 7e) recognized *Bastropia* as a distinct genus, and future work might confirm his assertion. Each species of *Bastropia* is known only from a single specimen or just a few specimens, and all specimens are from siliciclastic sandstone (can be glauconitic) or siltstone.

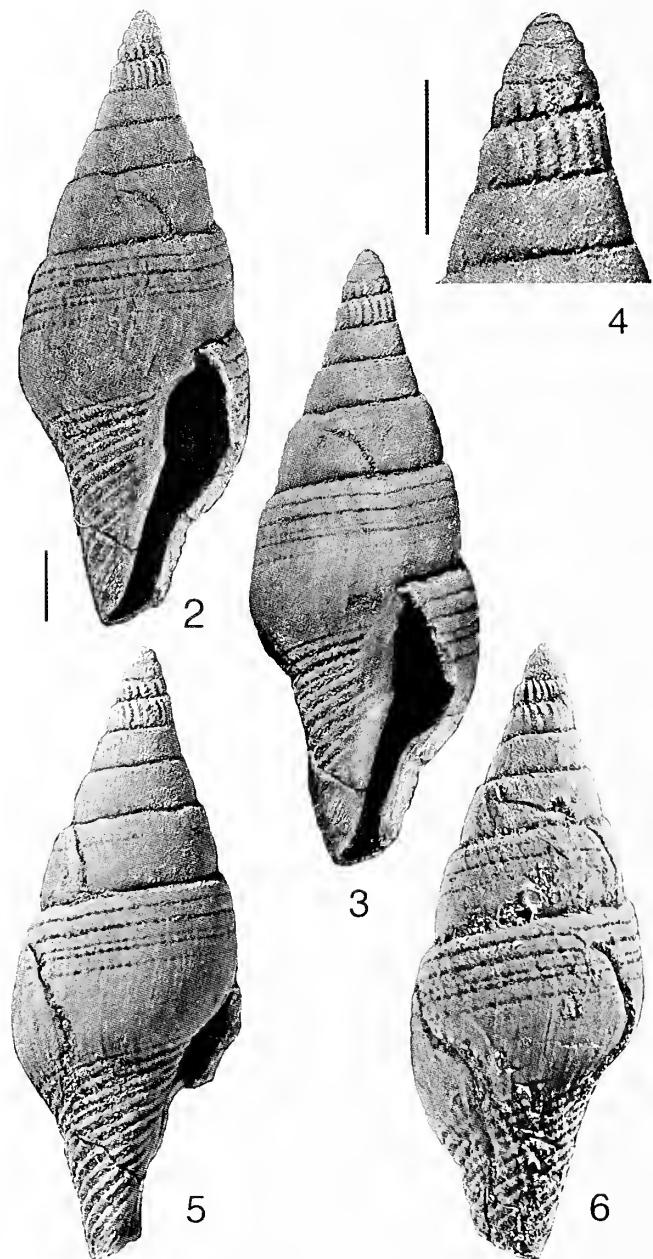
### *Bastropia llajasensis* new species

(Figures 2–6)

**Diagnosis:** *Bastropia* with a relatively low spire and wide pleural angle (40°), axial riblets on both second and third teleoconch whorls, incised spiral line(s) with or without pits commonly present near lower suture of lower spire whorls and near suture of last whorl, somewhat inflated last whorl, distinct siphonal fasciole.

**Description:** Shell small (8 mm height, 3 mm diameter), fusiform elongate. Entire shell comprised of nine whorls. Pleural angle 40°. Protoconch three whorls, overall narrowly conical, smooth; apical whorl low and domal with other two whorls slightly convex. Teleoconch six whorls, rather flat-sided except for more eonvex last whorl. Suture indented, imparting tabulate look to lower spire whorls. Axial sculpture confined to first and second teleoconch whorls (i.e., fourth and fifth whorls of entire shell) and consisting of approximately 18 narrow, closely spaced opisthocyst riblets extending from suture to suture and general alignment on both sides of suture. Spiral sculpture consisting of line(s) and ribs: Incised-spiral line(s) somewhat irregularly spaced, bearing many closely spaced pits between slightly raised growth lines, and confined to posterior part of penultimate and last whorls (three spiral lines on penultimate whorl and five on last whorl); spiral ribs confined to pillar (base of last whorl). Aperture narrow and long, widest posteriorly and with distinct constriction anteriorly. Outer lip missing. Inner lip with thin callus. Pillar long and with approximately 12 prominent spiral ribs; those on central part of pillar have “plicate appearance” underneath callus and onto inner lip but not extending very far into aperture. Pillar with small but distinct siphonal notch. Siphonal canal not bent. Growth line on spire whorls prosocline; growth line on last whorl parasigmoidal near suture but prosocline on pillar; intersection of growth lines and spiral ribs on pillar near columella producing weak cancellate shell-surface structure.

**Holotype:** LACMIP (Natural History Museum of Los Angeles County, Invertebrate Paleontology Section) 14514.



**Figures 2–6.** *Mitrella (Bastropia) llajasensis* new species. Holotype LACMIP 14514, LACMIP loc. 41604, height 8 mm.  
 2. Apertural view. 3. Apertural view turned slightly left. 4. Closeup of tip (height 1 mm) shown in previous figure. 5. Left-lateral view. 6. Abapertural view. Scale bars = 1 mm.

**Type Locality:** LACMIP 41604, in greenish-brown siltstone, on north side of paved road leading to a large water tank on east side of mouth of Runkle Canyon, near intersection with Sequoia Street, Santa Susana Quadrangle, 7.5-minute, photorevised 1969, south side of Simi Valley, Ventura County, southern California (Figure 1). Collector: R.L. Squires, March 27, 1999.

**Geologic Age:** Late early Eocene.

**Distribution:** Upper Ypresian Stage (equivalent to provincial lower “Domengine Stage”) part of the Llajas Formation, lower middle part within the “transgressive shallow marine” deposits, southern Simi Valley, Ventura County, southern California.

**Etymology:** Named for the Llajas Formation.

**Discussion:** A single specimen was found. It shows excellent preservation, except that it has undergone some post-depositional crushing. There are cracks in the shell (see Figure 5), and its outer lip is broken off. It is unfortunate that the interior morphology of the outer lip of the specimen cannot be determined, thus it cannot be determined if it represents a juvenile or an adult.

The new species differs from *Bastropia bastropensis* (Harris, 1895: 74, pl. 8, fig. 2; Palmer, 1937: 283, pl. 37, figs. 1, 7), from the lower middle Eocene Weches Formation in Bastrop County, Texas and also questionably from middle Eocene strata in Mississippi (Palmer and Brann, 1966: 774), by having a smaller shell, wider pleural angle, lower spire, no incised-spiral line anterior to the suture, incised spiral lines with pits near the suture between the penultimate and last whorls, last whorl more swollen, spiral ribs on pillar not as high up on the shell, central part of pillar with a “plicate appearance,” and the presence of a siphonal fasciole.

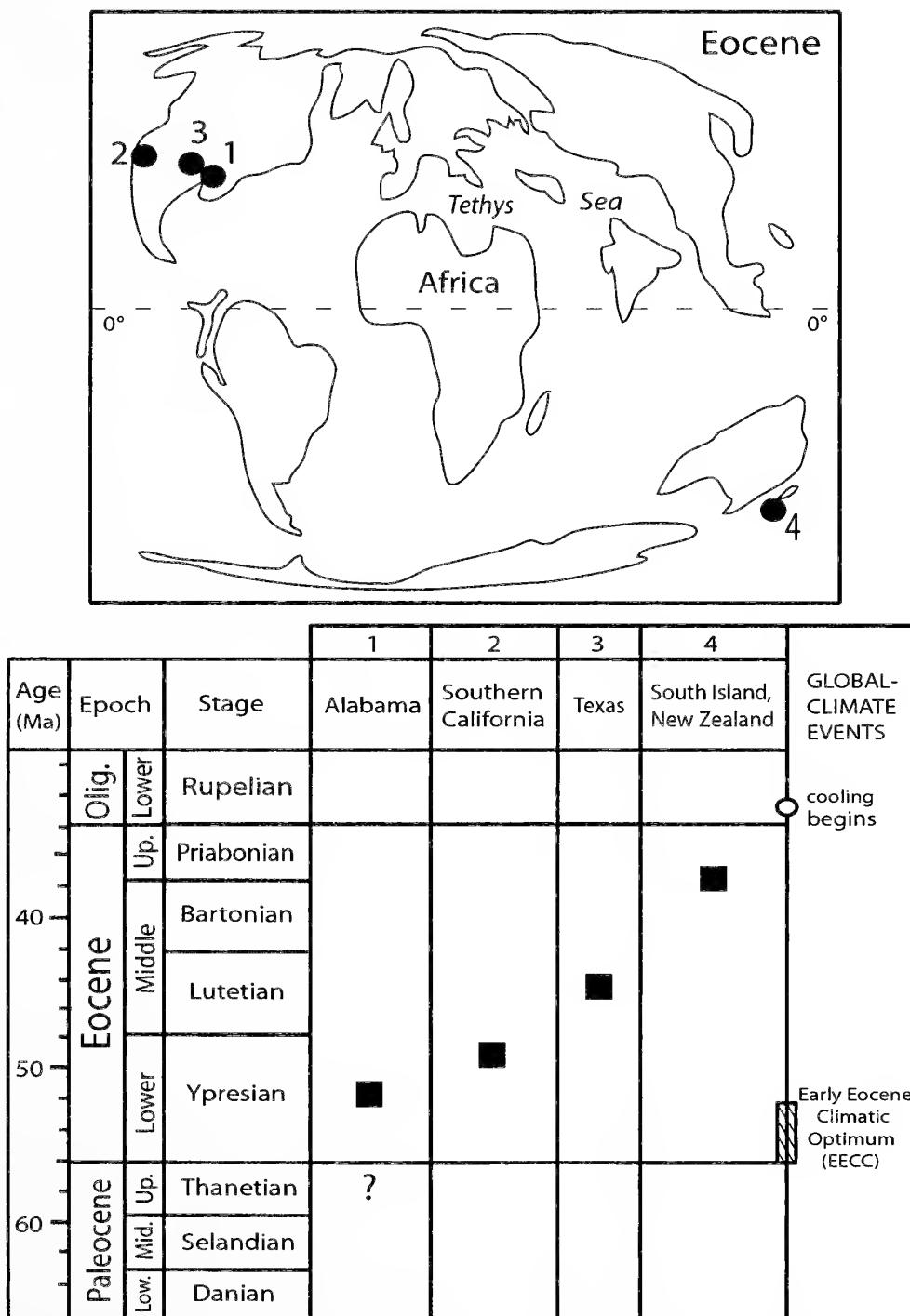
The new species differs from *Bastropia mackayi* (Suter, 1917: 43–44, pl. 5, fig. 12; Maxwell, 1992: 130, fig. 7e), from South Island, New Zealand, by having a smaller shell, wider pleural angle, lower spire, no incised spiral line on ante-penultimate whorl, additional incised spiral lines (but with pits) on last whorl and penultimate whorls, fewer spiral ribs on pillar, shorter posterior part of aperture, more inflated last whorl, and the presence of a siphonal fasciole. According to Maxwell (1992), *B. mackayi* occurs in either upper middle Eocene (upper Lutetian) or upper middle Eocene (Bartonian) strata, thus making *C. (B.) mackayi* the youngest known *Bastropia*.

The new species differs from *Bastropia subfraxa* (Harris, 1899: 58–59, pl. 7, fig. 11), from the lower Eocene (Ypresian) Bashi Member of the Hatchetigbee Formation Member in Alabama (Palmer and Brann, 1966: 512 [as *Astyris subfraxa*]), by having a smaller shell, wider pleural angle, lower spire, presence of spiral sculpture on the posterior part of penultimate and last whorls, and a more inflated last whorl. A questionable occurrence of *B. subfraxa* is from the Tuscaloosa Formation, Landing Marl Member, in Alabama (Toulmin, 1977: table 2). According to Dockery (1986: fig. 1), this member is near the late Paleocene (Thanetian)/early Eocene (Ypresian) boundary.

The presence of axial riblets on the upper spire of *Mitrella (Bastropia) llajasensis* new species resembles those on the incomplete paratype of the early Eocene columbellid that Garvie (1996) identified as *Mitrella (Clinurella) nuttalli* (Garvie, 1996: 68–69, pl. 14, fig. 17) from the lower Eocene Marquez Member of the Reklaw Formation in Texas. The new species differs from

Garvie's paratype, which consists of only the upper spire, by not having near the suture one or more relatively wide spiral ribs with prominent grooves in the interspaces. On the holotype (an adult specimen) of *M. (C.) nuttalli* (see Garvie, 1996: pl. 14, figs. 15–26), whose uppermost spire whorls have been eroded, these spiral ribs and grooves

become even more prominent on the penultimate and last whorls. *Bastropia llajasensis* new species differs also from the holotype of *M. (C.) nuttalli* by having a narrower shell, incised-spiral lines anterior to the suture, pits on these spiral lines, absence of prominent spiral ribs with sunken (flat-bottomed) interspaces on the



**Figure 7.** Global paleobiogeographic distribution and associated ranges of *Bastropia* (plotted in order of first-appearance datum); data derived from Table 1. Geologic time scale, stage ages, and timing of global-climatic events from Gradstein et al. (2012). Land-mass positions from Smith et al. (1994). Numbers at top of columns refer to geographic regions and primary sources of data: 1, Harris (1899), Palmer (1937), and Toulmin (1977). 2, present study. 3, Harris (1895). 4, Maxwell (1992).

anterior half of the last whorl, a more elongate pillar, narrower posterior part of aperture, and a more constricted siphonal canal. Although the outer lip is missing in the new species, the holotype of *M. (C.) nuttalli* has an outer lip interior with denticles. The holotype of *M. (Clinurella) nuttalli* is much more similar to the type specimen of the columbellid identified by Cossmann (1886) as *Mitrella (Columbellopsis) biarata* (Cossmann, 1886: 232–234, pl. 10, fig. 3, two views), from middle Eocene (Lutetian) strata in France. In addition, as noted by Garvie (1996: 68), *M. (Clinurella) nuttalli* is similar to *Mitrella (Clinurella) bucciniformis* (Heilprin, 1879: 213, pl. 13, fig. 7) and *Mitrella (Columbellopsis) mississippiensis* (Meyer and Aldrich, 1886: 43, pl. 38, figs. 16, 17, 21, 22).

The new species differs from the earlier mentioned Baja California species *Mitrella bacata* and *M. caulerpae*, which have axial riblets on the first one or two teleoconch whorls, in the following ways: Elongate-fusiform shell with a long anterior canal that is constricted anteriorly, indented sutures, subsutural-spiral sculpture consisting of pitted, incised-spiral lines on the penultimate and last whorls.

The only other known Paleogene columbellid from the northeast Pacific region is *Mitrella (Mitrella) blackhillsensis* Squires and Goedert (1994: 261, figs. 21–23), based on two specimens, from shallow-marine strata in the middle lower Eocene (“Capay Stage”) Crescent Formation in the Black Hills, Thurston County, southwestern Washington. Both specimens, however, are missing their upper spire, thus positive assignment of this species to a subgenus is not possible until more complete specimens are found. This Washington species is very similar to *Mitrella sensu stricto* in having an unsculptured shell (except for spiral ribs on the pillar), a short anterior canal, denticles on the interior of the outer lip, and a “varix”-like swelling preceding the outer lip. *Mitrella (Bastropia) llajasensis* n. sp. differs from this Washington species by having a large size, more slender shell, indented suture on spire, tabulate appearance to the spire whorls, much longer siphonal pillar, spiral sculpture on the posterior part of the penultimate and last whorls, no posterior channel-like indentation in the aperture, and no indication of a “varix”-like swelling preceding the outer lip.

#### PALEOBIOGEOGRAPHIC IMPLICATIONS

The details of the geologic range and locale of each of the four known species of *Bastropia* are given in Table 1 and are shown diagrammatically in Figure 7. As discussed earlier, a late Paleocene occurrence of *Bastropia* in Alabama is questionable. The earliest known documented record of this subgenus is early Eocene (middle Ypresian) in Alabama, and by the middle Eocene, it had spread westward into nearby Texas.

From the late Paleocene through middle Eocene, there were pulses of immigration of many shallow-marine, warm-water (thermophilic) mollusks and other

marine organisms into the northeast Pacific region. Most arrived from the Old World Tethyan Sea, Gulf Coast, and Caribbean Sea regions by means of westward-flowing currents that passed through a low-latitude seaway (Squires, 1987). The nearness in time between the earliest confirmed record of *Bastropia*, in the early Eocene in Alabama, and when it showed up in southern California, in the late early Eocene, supports the conclusion that *Bastropia* arrived in southern California from the Gulf Coast. Its dispersal would have been greatly facilitated if its larvae had planktotrophic development. This scenario is likely because its protoconch, which consists of three smooth whorls, is similar to those of previously mentioned (see “Discussion” of genus *Mitrella*) inferred planktotrophic species of *Mitrella* (e.g., the extant *Mitrella pallaryi* and a Miocene species). The southern California arrival of *Bastropia* was closely associated with a warming event called the “Early Eocene Climatic Optimum” (EECO), 51–53 million years ago (Figure 7). During this event, global temperature reached a long-term maximum (Zachos et al., 2008), and there was a global-sea-level rise (Miller et al., 2011), which would have expedited the dispersal of marine organisms.

With the exception of a species in South Island, New Zealand, *Bastropia* is restricted to North America. This New Zealand occurrence is of late middle Eocene age (Bartonian) and represents the youngest occurrence of this subgenus. It also provides limited evidence that *Bastropia* had an amphitropic distribution (Figure 7). The route of dispersal that *Bastropia* took to reach New Zealand cannot be determined based on current information.

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# Reinstatement of *Leda rhytida* Dall, 1908 and its reallocation into *Propeleda* (Bivalvia: Nuculanidae)

Marina GÜLLER

División Invertebrados

Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”  
Av. Ángel Gallardo 470  
(C1405DJR), Buenos Aires, ARGENTINA  
mguller@maen.gov.ar

Diego G. ZELAYA

Departamento de Biodiversidad y Biología Experimental  
Facultad de Ciencias Exactas y Naturales – UBA  
Ciudad Universitaria, Pab. 2, Lab. 31  
(C1428EHA), Buenos Aires, ARGENTINA  
dzelaya@bg.fcen.uba.ar

## ABSTRACT

In 1908, Dall described “*Leda*” *rhytida* as occurring off Acapulco, Mexico. The species was never figured, and has no subsequent published records. Despite that, it appears mentioned by several authors in check-lists. The identity of this species appears as controversial in the literature: some authors emended the type locality to either eastern South America or Chile, and the species was regarded either as a possible synonym of *Propeleda longicaudata* (Thiele, 1912), or considered as a *nomen dubium*. The aims of this study are to determine the actual provenance of the type material, to provide a proper redescription of the species, and to revise its generic placement and current status. The study of the syntypes and additional material from museum collections reveals that the species actually comes from southern Chile. Based on the elongated shell outline and distinctive hinge morphology, the species is here reallocated into *Propeleda*. Comparison of this species with *P. longicaudata* establishes that *P. rhytida* is a distinct and valid species.

**Additional Keywords:** Protobranchia, Nuculanoidea, Magellan Region, Chile, Taxonomy

## INTRODUCTION

*Leda* (*Leda*) *rhytida* Dall, 1908 is among the numerous new bivalve species described from the collections made by the U.S. ALBATROSS expedition along the Americas. The original description is poor and lacking in detail, and the species was never figured. According to Dall (1908) the species was collected “off Acapulco, Mexico, in 141 fathoms”, at ALBATROSS station 3422, and the type material was deposited at the United States National Museum [National Museum of Natural History, Smithsonian Institution], under number “122,918”. After examining the type material, Keen (1971) detected an error in the type locality originally indicated by Dall (1908). Keen stated that the true provenance of the species was “Patagonia, eastern South America” (sic). In contrast, Bernard (1983) indicated the type locality to be

“Chile”. Despite that, Zamorano and Hendrickx (2012) repeated “Acapulco” as the type locality. Apart from the original collection, no new records for the species are known. Recently, Coan and Valentich-Scott (2012) suggested that *Leda rhytida* could correspond to a synonym of *Propeleda longicaudata* (Thiele, 1912), a species described from the Gauss Expedition in eastern Antarctica, but currently regarded as widely distributed in Antarctic and sub-Antarctic waters (Dell, 1964; 1990; Villarroel and Stuardo, 1998). However, Bouchet (2014) regarded *Leda rhytida* as a *nomen dubium*. The aims of this contribution are to clarify the identity and precise provenance of *Leda rhytida*, to provide a proper redescription of the species, and revise its generic placement and its affinity with *Propeleda longicaudata*.

## MATERIALS AND METHODS

We examined photographs of the type material of *Leda rhytida* and *Leda longicaudata* (the latter currently treated in the genus *Propeleda*), housed respectively at the National Museum of Natural History, Smithsonian Institution (USNM), Washington, and Zoologisches Museum Berlin (ZMB). Additional material comes from the collection of the Museo de Zoología de la Universidad de Concepción (MZUC), Chile, and material sampled by the authors at the Beagle Channel and the South Shetland (61°23'45" S, 55°26'33" W) and South Orkney (60°58'53.4" S 43°26'42.6" W) (sub-Antarctic and Antarctic waters), currently housed at the Museo de La Plata (MLP), Argentina.

Shells were measured according to the parameters and ratios indicated by Kamenev (2014), by using an ocular micrometer mounted on a stereoscopic microscope, and a caliper for larger animals. Text abbreviations are: A, length anterior to beaks; H, maximum height perpendicular to L; L, maximum shell length; W, shell width across closed specimens. Details of hinge plate and protoconch were studied with a Phillips XL-30 scanning electron microscope (SEM), at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN).

## SYSTEMATICS

Genus *Propeleda* Iredale, 1924

**Type Species:** *Leda ensicula* Angas, 1877 (OD)

***Propeleda rhytida* (Dall, 1908) new combination**  
(Figures 1–16)

*Leda (Leda) rhytida* Dall, 1908: 219 (listed only), 376 (description).

*Propeleda longicaudata* Thiele, 1912: Villarroel and Stuardo, 1998: 142, figs. 113, 114 (in part).

**Redescription:** Shell club-shaped, delicate, moderately large for genus (max. observed  $L = 13.2$  mm), elongate ( $H/L = 0.44 \pm 0.01$ ,  $n = 8$ ), compressed ( $W/H = 0.49 \pm 0.02$ ,  $n = 8$ ), slightly gapping posteriorly; equivalve; markedly inequilateral: anterior end short, widely curved; posterior end projected into a curved rostrum, three to four times longer than anterior end (Figures 1–13). Anterodorsal margin consisting of a very short, almost horizontal section near beak, followed by a longer, obliquely sloping distal section, which is widely arched to slightly straight; both parts continuous or forming a weak angulation (Figures 1–8). Anterior margin evenly curved, joining anterodorsal margin in a slight angulation and continuous to ventral margin. Ventral margin markedly convex at anterior half and nearly straight at posterior half (Figures 1–8). Posterior (rostral) margin somewhat convex, forming well-marked angles at junctions with posterior part of dorsal and ventral margins. Posterodorsal margin long, slightly to markedly concave (Figures 1–8). Umbones opisthogyrous, located on anterior third ( $A/L = 0.29 \pm 0.02$ ,  $n = 10$ ), only slightly raised from dorsal margin. Two strong carinae running at posterior area of shell, along rostrum: one extending from umbo to junction of ventral and posterior margins, another from umbo to junction of postero-dorsal and posterior margins (Figures 1–8). Shallow sulcus between these carinae present. Anterior and central areas of shell sculptured with regularly distributed, rounded, commarginal cords, separated by narrow interspaces. These cords extend over two posterior carinae and into sulcus. Escutcheon large, well-defined by prominent dorsal carina, sculptured with faint lines (Figure 9). Lunule not differentiated. Prodissococonch small, about 165  $\mu$ m long, D-shaped, sculptured with a polygonal, net-like pattern (Figure 14). Periostracum thin, well-adhered, greenish-brown in wet specimens, straw-yellow when dry (Figures 1–8). Inner shell surface white, glossy, with a strong ridge extending along rostrum from umbo to approximately half of posterior margin, separating inhalant and exhalant siphons (Figures 10–13). Pallial sinus short, extending up to half of posterior adductor muscle (Figure 12). Anterior adductor muscle scar ovate, perpendicular to hinge; posterior adductor muscle scar narrower and smaller than anterior one, parallel to hinge plate. Hinge plate narrow, taxodont, with two series of teeth interrupted beneath beaks (Figures 12, 13). Anterior

series composed of about 15 teeth, posterior series with about 27 teeth, regarding larger specimens. Teeth variable in size and morphology within each series. Anterior series: first two teeth closest to beak, low, U-shaped; first evenly narrow, second with stronger ventral part (Figures 15, 16). One or two following teeth almost straight and lamellar. Subsequent teeth V-shaped, with ventral part gradually longer, increasing in size and height, sharply cusped. Most distal tooth greatly reduced in size. Posterior series: five to eight teeth closest to beaks lamellar, similar in solidness (Figures 15, 16). Internal ligament stout, posterior to beaks, slightly larger than resilifer, which is triangular, oblique, posteriorly directed. External ligament narrow, elongated, amphidetic, larger anteriorly and partially sunken below beaks (Figures 15, 16).

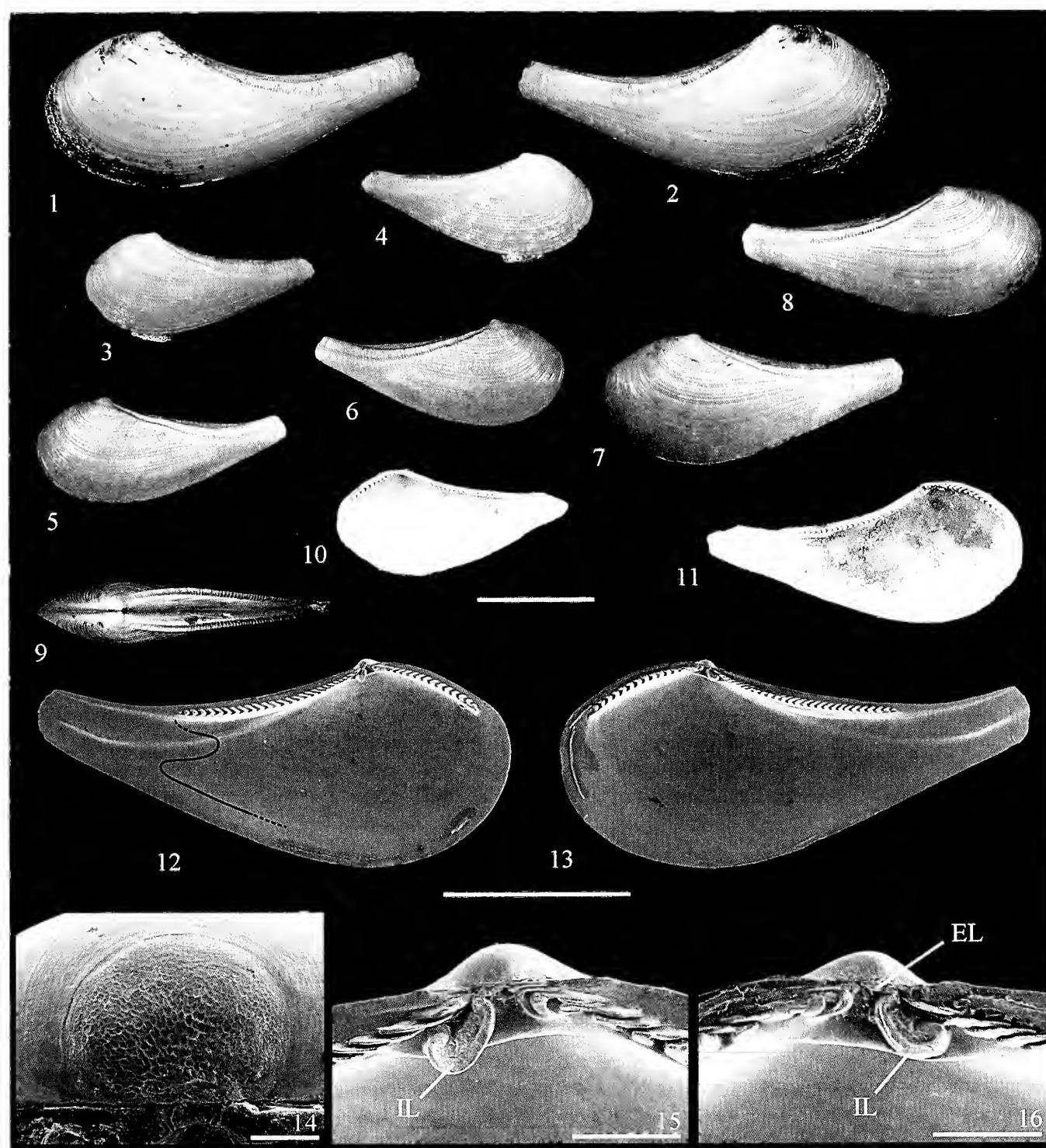
**Type Locality:** [Herein emended] U.S. ALBATROSS station 2783,  $51^{\circ}02'30''$  S,  $74^{\circ}08'30''$  W, west coast of Patagonia, 141 fathoms [=256 m].

**Type Material:** 8 syntypes (USNM 96918).

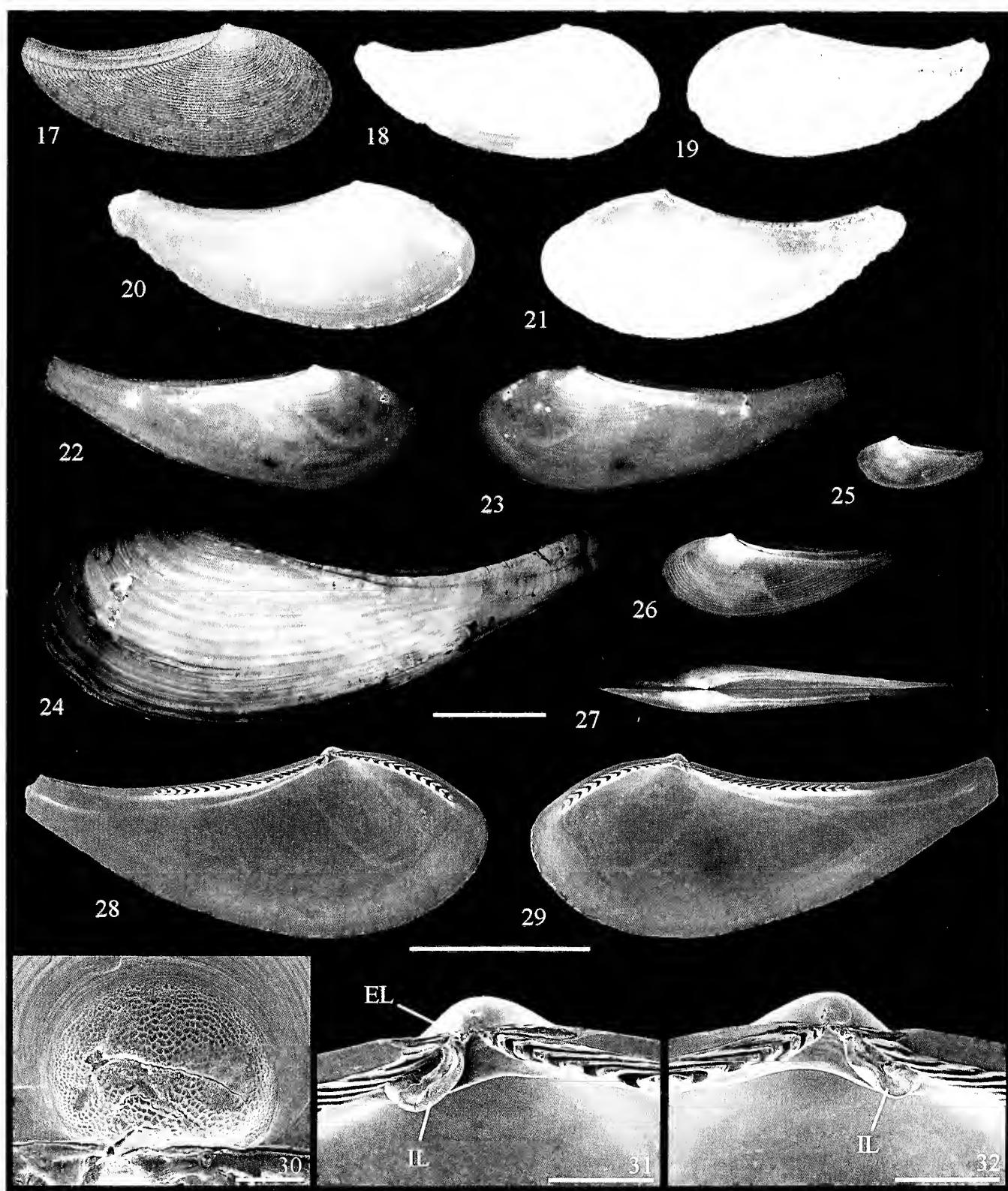
**Material Examined:** MZUC 10406, 1 specimen,  $50^{\circ}03' S$   $74^{\circ}41' W$ , Isla Tobar, 200 m; MZUC 4642, 8 specimens, and MZUC 4610, 19 valves,  $50^{\circ}09'55''$  S  $74^{\circ}43'75''$  W, Confluence Canales Concepción and Trinidad, 390–460 m; MZUC 4627, 1 specimen and 4 valves, same data as previous lot, but 460 m; MZUC 4646, 4 specimens and 4 valves,  $51^{\circ}00'50''$  S,  $74^{\circ}14'10''$  W, Puerto Bueno, Canal Sarmiento, 215–220 m; MLP Ma14041 1 specimen,  $54^{\circ}52' S$ ,  $68^{\circ}28' W$ , Bahía Lapataia, Beagle Channel, 120–138 m.

**Distribution:** Southern Chile and Beagle Channel, living at 120–460 m depth.

**Remarks:** Some discrepancies arise when comparing the original labels of the material currently identified as type of *Leda rhytida* (at the USNM) to information in the original description, in particular in relation to the repository number and the provenance of the types. The repository number mentioned by Dall (1908) ("USNM 122,918") actually corresponds to the holotype of *Leda lobula* Dall, 1908, another species described by that author in the same work. Dall indicated that this latter species also originated from ALBATROSS station 3422 (off Acapulco, Mexico). In addition, Dall did not provide a repository number for *Leda lobula*. The specimen in lot USNM 122918 agrees with the original description of *Leda lobula*, particularly differing from *Leda rhytida* by having an "ovate shape", with both anterior and posterior ends "rounded" (Dall, 1908: 375). In contrast, the original description of *Leda rhytida* refers to an "elongate-ovate" shell, with the anterior end rounded and the posterior one "produced" in a "strongly recurved rostrum". This set of characters is in accordance with the shell morphology of specimens in lot USNM 96918, currently labeled as syntypes of *L. rhytida* (Figures 1–4), whose label reads "Station 2783, west coast of Patagonia". Thus, it seems clear that there was an error in the published information of repository numbers and provenance



**Figures 1–16.** *Propeleda rhytida*. **1–4, 10, 11.** Four syntypes of *Leda rhytida* (USNM 96918). **1–4.** External views. **10, 11.** Internal views. **5–9, 12–16.** Specimens from  $50^{\circ}09'55''$  S,  $74^{\circ}43'75''$  W, southern Chile (MZUC 4642). **5–8.** External views. **9.** Dorsal view. **12, 13.** Internal views (pallial sinus shown in black line on Figure 12). **14.** Detail of prodissoconch. **15, 16.** Details of hinge plate. **15.** Left valve. **16.** Right valve. Scale bars: 1–11 = 5 mm; 12, 13 = 5 mm; 14 = 50  $\mu$ m; 15, 16 = 500  $\mu$ m. Abbreviations: IL = internal ligament; EL = external ligament.



**Figures 17–32.** *Propeleda longicaudata*. 17. Original figure by Thiele (1912). 18–21. Two syntypes of *Leda longicaudata* (ZMB 63104). 18, 20. External views. 19, 21. Internal views. 22–32. *Propeleda* cf. *longicaudata*. 22, 23, 27. Specimens from South Orkney (MLP 7467). 24–26, 28–32. Specimens from South Shetland (MLP 7468). 22–26. External views. 27. Dorsal view. 28, 29. Internal views. 30. Detail of prodissococonch. 31, 32. Detail of hinge plate. 31. Left valve. 32. Right valve. Scale bars: 17–27 = 5 mm; 28, 29 = 5 mm; 30 = 50  $\mu$ m; 31, 32 = 500  $\mu$ m. Abbreviations: IL = internal ligament; EL = external ligament.

of the species. Keen (1971) already detected such error, although she mistakenly wrote “**eastern** South America” instead of “**western** South America” when emending the type locality. Bernard (1983), on the contrary, did refer to a locality on the Pacific coast, but was ambiguous in stating “Chile”.

Based on the original label of the syntypes, the provenance of “*Leda*” *rhytida* is here emended to “51°02'30" S, 74°08'30" W, west coast of Patagonia” (which corresponds to ALBATROSS station 2783). Study of additional (conspecific) specimens from southern Chile and the Beagle Channel allows us to confirm the occurrence of the species in that area, and the nominal species is no longer regarded as a *nomen dubium* (as suggested by Bouchet, 2014) but as a valid species.

**GENERIC ALLOCATION OF THE SPECIES:** The genus *Leda* Schumacher, 1817 in which *L. rhytida* was originally described is an objective junior synonym of *Nuculana* Link, 1807. Allen and Hannah (1986) defined this genus by the presence of robust and “moderately” posteriorly elongated shells. Allen and Sanders (1996) added as a diagnostic character the presence of a robust hinge with V-shaped teeth and a small ligament, and the absence of an internal posterior ridge running from umbo to posterior margin. The fact that all teeth are V-shaped in this genus can be confirmed from the illustrations of *Nuculana pernula* (Müller, 1779) in Oliver et al. (2010) (this species is currently regarded as a senior synonym of *Arca rostrata* Brugière, 1789, the type species of *Nuculana*). In addition, these photographs show that the internal ridge is extremely short in this species, being present only in the distal part of the rostrum.

This set of characters does not match those present in “*Leda*” *rhytida*, which has delicate, very posteriorly elongated shells, with a long internal ridge extending from the umbo to posterior margin, and bearing a large internal ligament and differentiated lamellar teeth near the beak. In contrast, the characters present in “*Leda*” *rhytida* are in agreement with those present in *Leda ensicula* Angas, 1877, the type species of *Propeleda* Iredale, 1924 (Huber, 2010; Kamenev, 2014). Consequently, “*Leda*” *rhytida* is here reallocated into *Propeleda*. The distinction of *Propeleda* from other nuculanid and siliculid genera was discussed by Huber (2010) and Kamenev (2014).

**AFFINITIES BETWEEN PROPELEDA RHYTIDA AND PROPELEDA LONGICAUDATA:** Coan and Valentich-Scott (2012) suggested that *Propeleda rhytida* (as *Leda rhytida*) could correspond to a synonym of *Propeleda longicaudata* (reported by the authors under *Nuculana*). The study of the syntypes of the latter species (Figures 17–21) reveals that both species show morphological resemblance. Nonetheless, *P. rhytida* may clearly be distinguished by having shells with shorter and more broadly rounded anterior end, more projected ventral margin and posterior rostrum, stronger and more spaced commarginal sculpture, and the two posterior carinae stronger (wider

and higher) than *P. longicaudata*. These differences lead us to consider the two taxa as distinct species.

*Propeleda longicaudata* is currently regarded as a widely distributed Antarctic and sub-Antarctic species, occurring in South Georgia, South Orkneys, South Shetlands, Weddell Sea, Ross Sea and East Antarctica (Dell, 1964; 1990; Hain, 1990; Aldea and Troncoso, 2010). The study of two lots of “*P. longicaudata*” from South Orkney and South Shetland (MLP 7467, 7468, respectively) reveals some morphological differences between these specimens and the syntypes of that species, namely the presence of a consistently less recurved and longer rostrum, which consequently generates a more elongated shell outline (Figures 22–25, 28, 29). At present, the significance of these differences could not be determined, because the syntypes are represented by only 3 valves, and no additional specimens from the type locality were available to evaluate the intraspecific variability of this taxon. Therefore, we prefer to be conservative and refer to the South Orkneys and South Shetland specimens here studied as *Propeleda* cf. *longicaudata*. The specimens here studied of *P. cf. longicaudata* (Figures 22–32) also differ from *P. rhytida* by having less inflated shells ( $W/L = 0.16 \pm 0.01$ ,  $n = 10$  vs.  $W/L = 0.22 \pm 0.01$ ,  $n = 8$ ) and a minor number of posterior teeth, even when considering specimens of similar size (23 vs. 27 in specimens about 13 mm long). Moreover, in *P. rhytida* the lamellar teeth at the posterior series are shorter and stouter, and at the anterior series, the two teeth closest to the beaks are consistently stronger (Figs. 15, 16 vs. 31, 32), and the V-shaped teeth are taller and more delicate. Furthermore, judging from the material here available, *P. cf. longicaudata* reaches a larger size (23.8 mm vs. 13.2 mm long in *P. rhytida*).

*Propeleda longicaudata* was also previously reported as occurring in southern Chile by Villarroel and Stuardo (1998). However, the study of the specimens they mentioned (MZUC 4610, 4627, 4642, 4646) indicates that they were misidentified by those authors. The lots are here reassigned to *Propeleda rhytida*.

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# Shells and fossils collected by the earliest settlers of Jamestown, Virginia, USA

**Juliana M. Harding<sup>1</sup>**

Department of Marine Science  
Coastal Carolina University  
P.O. Box 261954  
Conway, SC 29528 USA  
jharding@coastal.edu

**Beverly A. Straube<sup>2</sup>**

Jamestown Rediscovery  
1365 Colonial Parkway  
Jamestown, VA 23081 USA

**Brittany L. Grimm**

**Geerat J. Vermeij**  
**Howard J. Spero**

Department of Earth and Planetary Sciences  
University of California Davis  
Davis, CA 95616 USA

## ABSTRACT

The discovery of an intact valve of the fossil bivalve *Chesapecten jeffersonius* and shells of three tropical snail species in a c. 1610 James Fort well speaks to the curiosity that European colonists brought to the New World. While implementing the Virginia Company of London's mandate to identify and secure profitable natural resources, the Jamestown, Virginia, colonists apparently also gathered interesting natural objects. The shells may have been collected either as personal souvenirs, much like modern-day tourists, or as curios destined for the lucrative European conchology market. *Chesapecten jeffersonius*, Virginia's state fossil, was collected locally as representatives can still be found in James River Pliocene deposits near Jamestown. In contrast, the tropical shells were likely brought to Jamestown in May 1610 by survivors of an English shipwreck on Bermuda. The shells from both Virginia and Bermuda were discarded in the fort's well by June 1610 as the settlers hastily prepared to permanently abandon Jamestown.

*Additional Keywords:* *Chesapecten jeffersonius*, *Lobatus gigas*, *Strombus pugilis*, *Cittarium pica*, Jamestown

## INTRODUCTION

The Virginia Company of London sent colonists to America to exploit natural resources including timber, iron, and, particularly, gold. Most of the initial exploratory efforts were focused upon finding resources that could reward Virginia Company shareholders with immediate investment returns (Horn, 2005). Gold was a top priority for the nascent colony, as reflected in Captain John Smith's lament that "there was no talke, no hope, no worke, but dig gold, wash gold, refine gold, load gold" (Smith, 1986a: 218).

Archaeological investigations of James Fort since 1994 by the Jamestown Rediscovery Project have uncovered

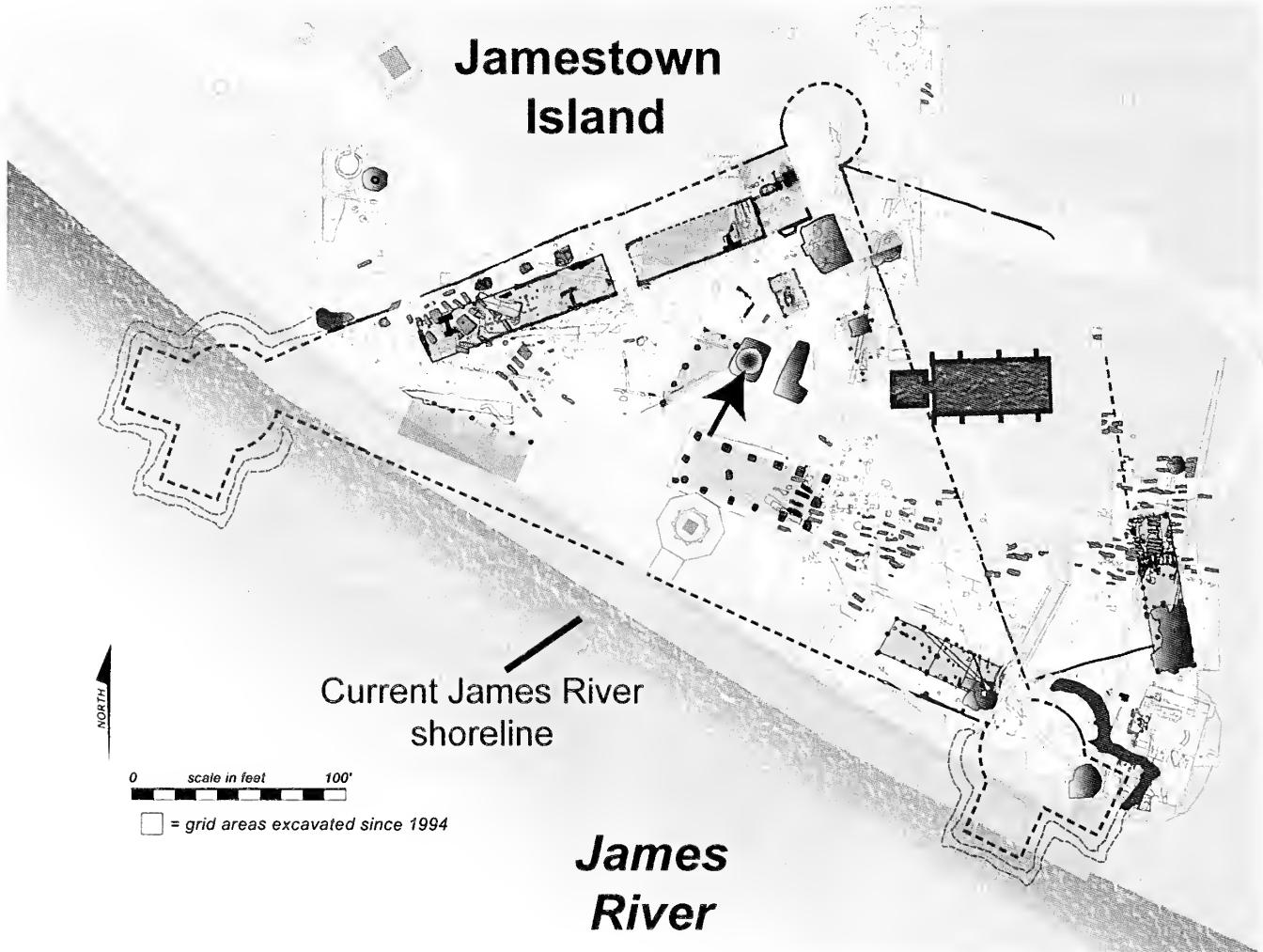
evidence that early endeavors to extract profitable resources included much more than the search for gold. Some of the undertakings included specialists from Germany producing glass; English metallurgists making trials of Virginia minerals that might alloy with English copper to make brass; and a tobacco pipemaker producing tobacco pipes from the local clay (Straube, 2004; Hudgins, 2005). The 17th-century Englishmen were also interested in New World flora and fauna that could be used for medicinal applications. Captain Gabriel Archer, writing in 1607 of Virginia's natural bounty, mentioned "Apothecary drugges of diverse sortes, some knowne to be of good estimacion, some strange, of whose vertue the salvages report wonders" (Archer, 1969: 102).

Botanical and biological specimens were also prized for being exotic. At the time of Jamestown's founding, European curiosity about the natural world resulted in a market for objects of nature, especially those from newly explored lands. *Naturalia* "was a commodity bought, sold, bartered, and exchanged—the centerpiece of a series of transactions that connected the world of commerce to the study of nature" (Findlen, 2002: 298). Nobles, wealthy gentlemen, and academics who could afford to do so, assembled these objects in cabinets of curiosities as eclectic reflections of status, records of travel, or tangible proof of their quest for knowledge. Indications of this pursuit for authentic naturalia have been discovered during archaeological excavations of James Fort's earliest contexts and particularly in the settlement's first well (Kelso et al. 2012: Structure 185).

In early June 1610, the well that had served as a water source for the inhabitants of James Fort for two years was quickly filled with half a million objects (Kelso et al., 2012, Figure 1). Jamestown was being abandoned, and these materials represented the remains of meals, the detritus of everyday life, and objects that were not considered valuable enough to transport to England. This action was precipitated by the preceding winter, dubbed by John Smith as the "starving time," which had claimed the lives of three out of four of the colonists and left many of the survivors sick and malnourished (Smith,

<sup>1</sup> Corresponding author

<sup>2</sup> Current address: 6 Valentine Court, Newport News, VA 23606, USA



**Figure 1.** Archaeological plan of James Fort (Courtesy of J. May, Jamestown Rediscovery Project, Preservation Virginia) on the current shoreline of the James River, Virginia. Black arrow identifies the Jamestown well (Structure 185) from which the shells were excavated.

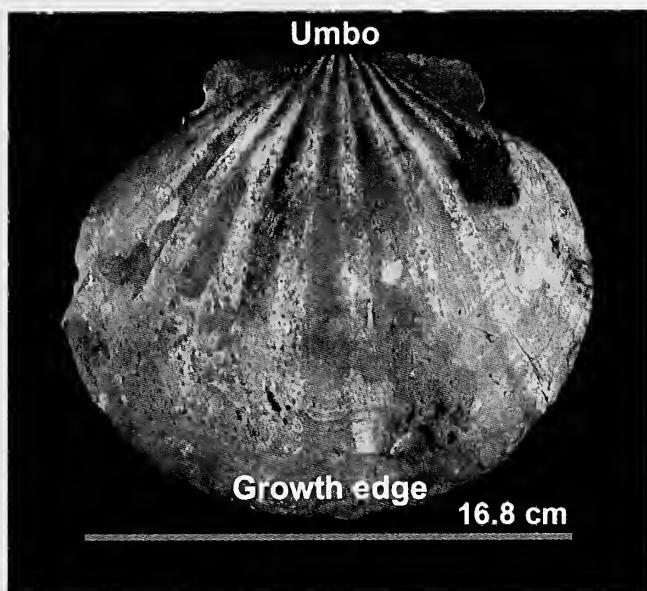
1986b: 340). With few prospects of obtaining food, Governor Thomas Gates decided to sail to Newfoundland where he hoped that the English fishing fleet could help transport colonists the rest of the way home. Gates did not want to attempt a transatlantic voyage from Virginia as his four small vessels were overloaded with over 150 colonists, the provisions needed for the voyage, the colony's weaponry, and "all the best things in the store," which hopefully could be sold for profit upon arrival in England (Strachey, 1973:76).

Four hundred years later, archaeological investigation of the c. 1608–1610 James Fort well revealed a variety of marine mollusk shells among the discarded items. The assemblage included an intact fossil *Chesapecten jeffersonius* valve (Say 1824) (Figure 2) as well as seventeenth-century specimens of tropical marine snails including the queen conch *Lobatus gigas* (Linneaus 1758) (Figure 3), the West Indian fighting conch *Strombus pugilis* (Linneaus 1758), and the West Indian

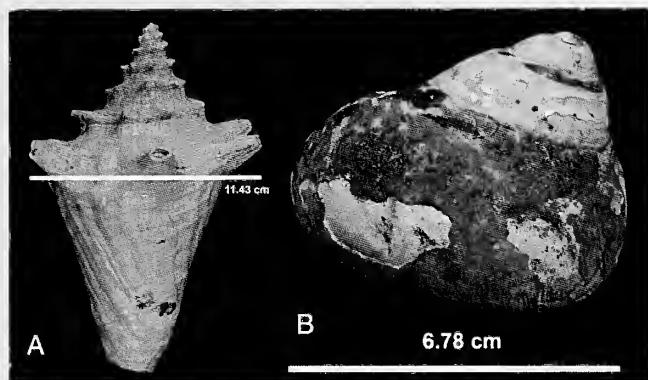
top snail *Cittarium pica* (Linneaus, 1758, Figure 3). The molluscan fauna recovered from this earliest Jamestown well offer a glimpse into undocumented pursuits in the early years of the colony.

#### DESCRIPTION OF THE SHELLS AND HYPOTHESES FOR THEIR ORIGINS

*Chesapecten jeffersonius* (Bivalvia) is a large temperate scallop that occupied the shallow subtropical continental shelf of North America during the Pliocene, 2–5 million years B.P. Today, these marine sediments are exposed across the mid-Atlantic US coastal plain due to the drop in post-Pliocene sea level after the expansion of the Antarctic ice sheet (Rovere et al., 2014). This scallop species is part of a unique faunal group used by geologists to characterize the Sunken Meadow Member or the oldest strata associated with the Yorktown formation.



**Figure 2.** The *Chesapecten jeffersonius* valve discarded in the earliest known Jamestown well as James Fort was being abandoned in June 1610. Courtesy of M. Lavin, Jamestown Rediscovery Project, Preservation Virginia.



**Figure 3.** Bermudan shells brought to the New World by SEA VENTURE survivors that were thrown away in the Jamestown well in June 1610 including *Lobatus gigas* (A) and *Cittarium pica* (B). Both courtesy of M. Lavin, Jamestown Rediscovery Project, Preservation Virginia.

The fossils used as the modern basis for this description were collected from cliffs directly downriver of Sunken Meadow Pond on the James River in Surry County, Virginia (Ward and Blackwelder, 1980) (Figure 4).

When Thomas Say (1824) established the formal taxonomic designation for this scallop (as *Pecten jeffersonius*), he relied on illustrations made by Martin Lister in 1687 (*Historiae Conchyliorum, Liber III: plate 167*; Ward and Blackwelder, 1975). Thus, these scallops have the distinction of being the first American fossils ever described (Ward and Blackwelder, 1975). Although this species has been extinct for ~4 million years (Krantz, 1991), *C. jeffersonius* has played a role in modern paleoenvironmental reconstructions (e.g., Krantz 1990), paleon-

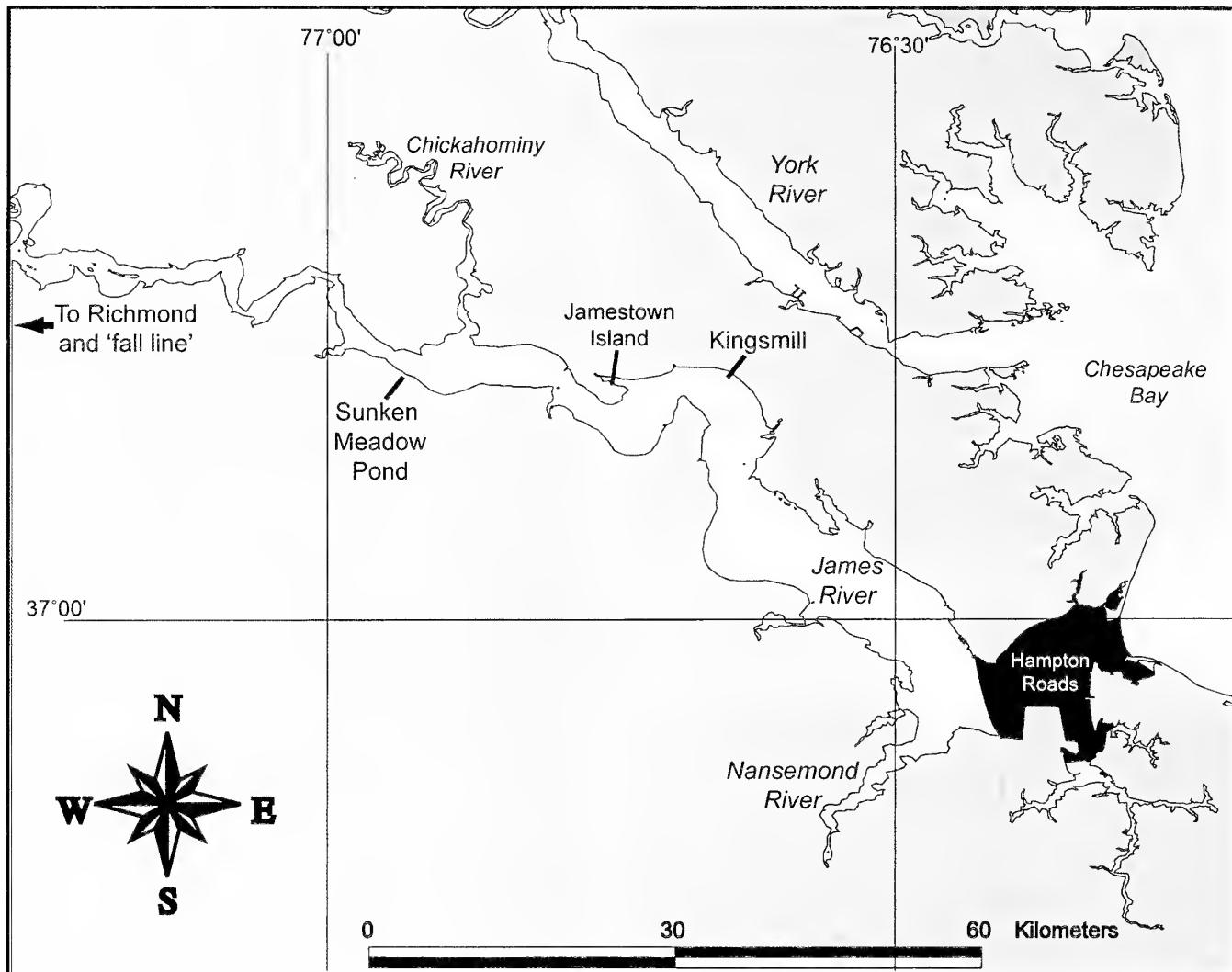
topological stratigraphic characterizations (e.g., Ward and Blackwelder, 1975: Zone 1 Yorktown Formation; Blackwelder, 1981: Sunken Meadow Member, Yorktown Formation), and now offers a window into Jamestown's early years.

Ward and Blackwelder (1975) characterized *Chesapecten jeffersonius* as having shell heights >12.0 cm where height is the longest distance from the umbo to the growth edge. The Jamestown *C. jeffersonius* valve is 15.6 cm high and 16.8 cm long (distance perpendicular to height, Figure 2). This height is greater than the largest valve height (13.77 cm) reported by Ward and Blackwelder (1975) and the *C. jeffersonius* from Kingsmill, Virginia, used by Krantz (1990, 10.3 cm shell height). The Sunken Meadow Member paleoenvironment was a temperate, marine habitat in which "many mollusks attained unusually large sizes" (Ward and Blackwelder, 1980: D35). Kingsmill is on a northern shore cliff downriver of Jamestown Island (Figure 4). At Kingsmill, as well as in other James and York River sites, fossils are deposited in the modern littoral zone, as they erode from Yorktown Formation stratigraphic layers, where they are easily collected.

James Fort was established on the banks of the James River, which served as the colony's major thoroughfare and source of seafood. In the summer of 1609, in an attempt to take pressure off Jamestown food and water sources, Captain John Smith dispersed colonists 32 km downriver to live on the "oyster banks" that flourished in the saltier water of Hampton Roads and to an Indian settlement near the mouth of the Nansemond River where the English traded copper for food (Archer, 1969, 282; Earle, 1978) (Figure 4). An additional 120 colonists were sent to the fresher water upriver near the 'fall line' of the James (Smith, 1998b: 220). It is probable that the colonists stopped during river trips to investigate food sources as well as to wait for favorable wind or tidal conditions to facilitate travel.

As the colonists grew more familiar with the region, they investigated inland areas as potential sources of mineral wealth and also to mimic the native Algonquin seasonal occupancy patterns. It is possible that the fossil scallop was collected on a trip between Jamestown Island and the temporary upriver settlement near the "falls". Sunken Meadows Pond and the adjacent cliffs, the type locality for the Sunken Meadow Member of the Yorktown formation (Ward and Blackwelder, 1980), are approximately 16 km upriver of Jamestown Island on the opposite shoreline (Figure 4). It is likely colonial travelers investigated these and other James River sites where Yorktown formation material was exposed during regular travel as well as when on exploratory expeditions.

A less likely scenario is that the scallop was discovered during Smith's initial exploration of the Chesapeake Bay in summer 1608 and retained as a souvenir. *Chesapecten jeffersonius* occurs in Yorktown formation deposits located along the track of Smith's second Chesapeake voyage (Jul.–Sep. 1608, Clark et al., 2007). The last legs of this voyage included areas with *C. jeffersonius* deposits



**Figure 4.** Map of the James River, Virginia, USA showing the likely collection sites for the fossil scallop in relation to Jamestown/James Fort with the Hampton Roads region (shaded) indicated for reference.

on the western Chesapeake shoreline south from the Patuxent River into the Rappahannock, Piankatank, Poquoson, Elizabeth, and Nansemond Rivers (Clark et al., 2007).

The possibility that the scallop was a gift to Smith from one of the Algonquin chiefdoms he visited is more intriguing but even less likely than the other scenarios. Although Virginia's native Algonquin tribes used small fossil gastropods (such as the marginellid *Prunum limatulum* (Conrad, 1834)) as embroidery ornaments for ceremonial robes (e.g., "Powhatan's Mantle", Rountree and Turner, 2002: 115–116), Algonquin use of *C. jeffersonius* was not documented by the early colonists.

Preservation of a large intact scallop shell through the rigors of James Fort life during the "starving time" is impressive. One can only wonder whether the original collector died and the fossil simply became another item to be discarded when the order was given to abandon the fort. While considered of value at one point, it was

deemed of little worth relative to food and colonists since space on the departing ships was limited. Other fossils (e.g., shark's teeth) have also been discovered by archaeologists in other James Fort contexts from the 1607–1610 period. Fossils would not have been recognized in the early 17th century as representing extinct ancient life but rather as minerals formed by natural processes in the earth, which sometimes resembled living organisms (Cook, 2003; MacGregor, 2007).

Shells of three tropical snail species were also deposited in the Jamestown well in June 1610. The tropical snails (Figure 3) are found neither in the Yorktown formation nor in modern Chesapeake habitats. In fact, *Cittarium pica* does not currently live in Bermuda. Shells of this species from Bermuda date from the Pleistocene, but are today (as in the 1600s) commonly inhabited by the terrestrial hermit crab *Coenobita clypeatus* (Fabricus, 1787; Olson and Hearty, 2013). These tropical shells were most likely collected in Bermuda between July 28, 1609

and May 10, 1610 (Strachey, 1973). These dates encompass the time span between the Bermuda wreck of the *SEA VENTURE*, carrying prospective Jamestown colonists, and the survivors' departure for Jamestown almost 10 months later. The shipwreck survivors, including the newly appointed governor, Sir Thomas Gates, arrived at Jamestown shortly before the colony's abandonment in June 1610. There was no other recorded contact between Jamestown and Bermuda prior to this date. Further, accounts of the voyage from Bermuda to Virginia do not mention any landfall, but it is possible that either the queen conch or the West Indian fighting conch might have been collected during a brief stop for provisions or water along the Southeast US coast since both species historically ranged as far north as Georgia (Abbott, 1974).

We hypothesize that the Bermudan shells were collected by the *SEA VENTURE* castaways as attractive curios, much like modern travelers pick up sea shells. Knowledge of the shells' intrinsic worth to collectors in Europe may have been another motivating factor for the colonists' interest in keeping these objects. The study of molluscan shells, known as conchology, developed as a scholarly discipline during the 17th century (Huxley, 2003). Shells from around the world could be sold to private European natural history collectors for a considerable profit. The discovery of specially gathered shells in the fort well speaks to the survival mentality of the remaining colonists when they abandoned Jamestown in June 1610.

## SUMMARY

Molluscan fauna recovered from the earliest Jamestown well offer a glimpse into undocumented pursuits on the part of the early English colonists relating to the developing commodification of natural objects. Virginia and its early 17th-century English settlement were part of the growing network of global trade that placed value and significance on the exotic, including objects of nature. A fossil *Chesapecten jeffersonius* was collected locally, most likely by a colonist exploring the James River in search of merchandisable commodities. Tropical snail shells gathered in Bermuda during the winter of 1609–1610 were sufficiently interesting and perhaps valuable, to be saved and transported by the *SEA VENTURE* shipwreck survivors to Jamestown in May 1610. Despite the ascribed values and significance that led to them being picked up initially, all of the shells were ultimately discarded in June 1610 during the swift abandonment of James Fort. This departure was only thirty hours in duration as the colony was providentially revitalized by the arrival of the colony's new governor with copious provisions and fresh settlers. But, in retrospect, if the settlement had not experienced this temporary major setback it is very unlikely that the fossil and tropical mollusks would have been discarded at Jamestown for archaeologists to find and interpret 400 years later.

## ACKNOWLEDGMENTS

The authors would like to acknowledge the staff of the Jamestown Rediscovery Archaeological Project, especially those involved in the excavation, curation, and interpretation of the well (Structure 185). These include Dr. W. Kelso, D. Schmidt, J. May, D. Givens, M. Lavin, M. Richardson, D. Smith, D. Gamble, and D. Warmke. BLG acknowledges the support of the University of California, Davis, Dept. of Earth Sciences, Durrell Fund during the completion of her M.S. research. We thank Dr. M.G. Harasewych for early discussions on the identification of the scallop and helpful information on Bermuda mollusks. We also thank C.T. Sailer for her comments on an earlier draft of this manuscript.

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# Two new species of *Tryonia* (Caenogastropoda: Cochliopidae) from the late Pleistocene of Coahuila, northern Mexico

Alexander Czaja

José Luis Estrada-Rodríguez<sup>1</sup>

Department of Biological Sciences

Juárez University of the State of Durango (UJED)

35010 Gómez Palacio

Durango, MEXICO

josefo7@hotmail.com

## ABSTRACT

Two new species of Pleistocene freshwater snails of the genus *Tryonia* Stimpson (1865) from Coahuila, northern Mexico, are described. One of them, *Tryonia hershleri* new species, belongs to a group of species that have shells with characteristic prominent axial ribs. The second species, *Tryonia pseudocircumstriata* new species, is similar to recent and fossil species from the Pecos River in the southwestern United States. Contrary to earlier practice, we propose to use different species names for Pleistocene and extant *Tryonia* from the Pecos River.

**Additional Keywords:** Late Quaternary, *Tryonia circumstriata*, *Tryonia stocktonensis*

## INTRODUCTION

Although little investigated, the desert regions of north-eastern Mexico contain abundant lacustrine sediments with rich late Quaternary molluscan faunas (Czaja et al., 2014a; 2014b). Specimens of *Tryonia pseudocircumstriata* new species were collected from eolian sediments (inland dunes) of an ancient paleolake that occupied a huge drainage basin in the central Laguna Region, Coahuila, Mexico (Figure 1). *Tryonia hershleri* was collected in the same region but from fluvial-lacustrine deposits.

These sites contain one of the most diverse molluscan faunas of the late Quaternary of northern Mexico, with countless specimens preserved mainly in dune sediments (Czaja et al., 2014a). The fossil material shows an excellent preservation that allows for detailed species description.

The genus *Tryonia* contains 33 recent aquatic species distributed mainly in western North America, with one species known from Guatemala and *Tryonia porrecta* from Hawaii. More than half of the species of *Tryonia* occur in the Chihuahuan Desert, where the genus shows

a high level of local endemism. However, many endemic species of *Tryonia* are endangered or already extinct because freshwater habitats are disappearing, mainly as a result of human activities (groundwater mining) (Hershler et al., 2011; 2014).

Fossil members of the genus have been described from the Miocene of Venezuela, Peru, Colombia, Brazilian Amazonia, and from the Pliocene of Guatemala (Wesselingh and Macsotay, 2006). Uncertain are Miocene records of *Tryonia* from the southwestern USA, but some of the Pliocene shells described as *Hydrobia* and *Calipyrgula* by Pilsbry (1935) from the Kettleman Hills, California, probably belong to *Tryonia* (R. Hershler, pers. comm.). So far, Pleistocene records of the genus had been known only from the United States (Hershler, 2001).

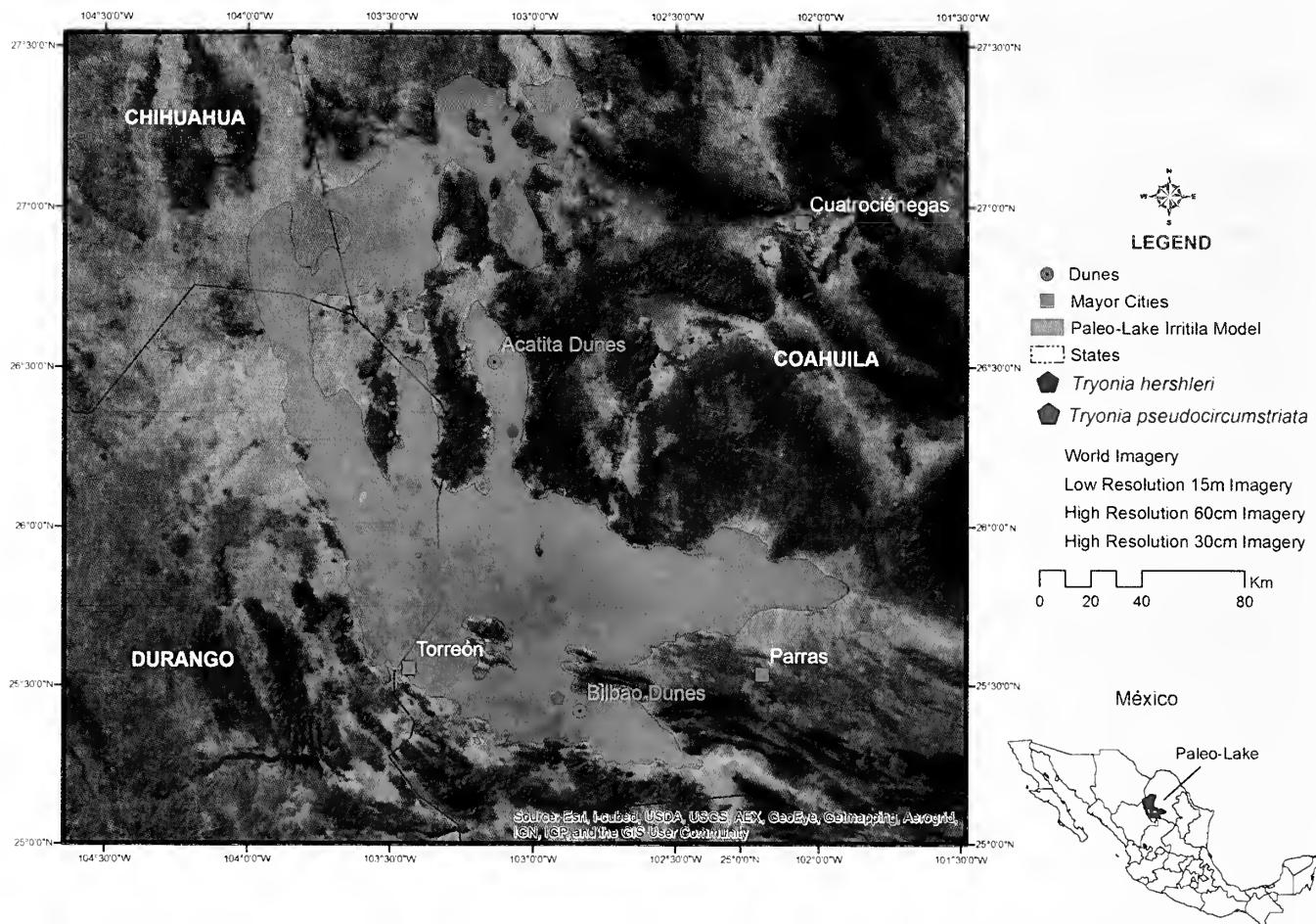
The aim of the present study is to describe the new species and to compare them with living and fossil members of the genus *Tryonia*. The present investigations form part of a broader study of fossil land and freshwater mollusks (ecology, systematics, and biogeography) from the region that begun in 2013 (Czaja et al., 2014a; Czaja et al., 2014b).

## MATERIALS AND METHODS

Shells of *Tryonia hershleri* new species were collected at Acatita Valley, Coahuila, Mexico, ca. 8 km north of Charcos de Risa ( $26^{\circ}16'53.77''$  N,  $103^{\circ}4'25.96''$  W). These shells were collected in Pleistocene deposits exposed along the western side of a road to Laguna del Rey. The shells derive from a gravel-sand layer of fluvial-lacustrine deposits and were collected directly from a cut of approximately 2 m thickness. Similar alluvial sandy gravel beds known from various sites in the vicinity have been dated as late Pleistocene ( $\sim 15,000$  BP,  $^{14}\text{C}$  dates) by Butzer et al. (2008).

The shells of *Tryonia pseudocircumstriata* new species were collected from dune sediments in the south part of the Paleo-Lake Irritila, Coahuila, 300 m W of the locality Gabino Vázquez ( $25^{\circ}26'17.45''$  N,  $102^{\circ}55'12.93''$  W).

<sup>1</sup> Corresponding author



**Figure 1.** Map of the *Paleolake Irritila* in Coahuila, Mexico showing the collecting localities of the new species described in this paper (modified from Czaja et al., 2014a).

These eolian dunes are of Holocene age but their fossil content is older and comes from late Pleistocene lacustrine sediments (Butzer et al., 2008; Czaja et al., 2014a).

Unconsolidated sediments of both sites were screened through 0.5 mm and 0.3 mm sieves. The fossils were photographed with a Zeiss AxioCam ERc5s microscope-camera. The collected material is housed at the Faculty of Biological Science of the Juarez State University of Durango (UJED), Campus Gómez Palacio.

#### SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1795

Subclass Caenogastropoda Cox, 1960

Superfamily Truncatelloidea Criscione and Ponder, 2013

Family Cochliopidae Tryon, 1866

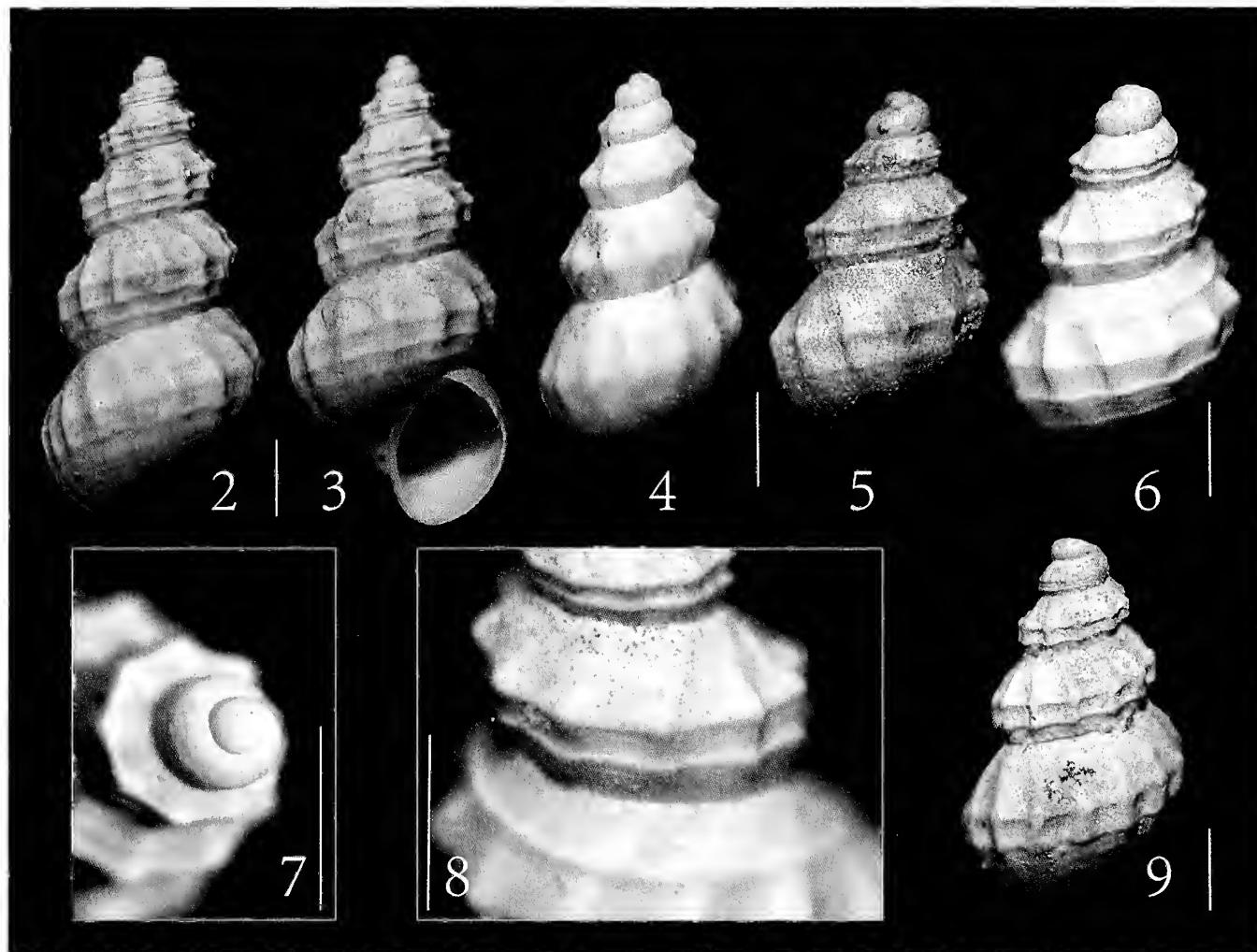
**Genus *Tryonia* Stimpson, 1865**

**Type Species:** *Tryonia clathrata* Stimpson, 1865 (by original designation).

***Tryonia hershleri* new species**  
(Figures 2–10, 16, Table 1)

**Diagnosis:** Shell medium- to large-sized, conical to turreted, with robust axial ribs, aperture ovate; distinguished from similar congeners by the pattern of shell sculpture (see taxonomic remarks).

**Description:** Shell medium-sized, conical to turreted, having 4.75–6.25 weakly shouldered whorls, strongly but variable sculptured. Height 3.50–5.95 mm, width 2.05–2.90 mm (shell measurements in Table 1). Protoconch smooth. Sculpture from low to robust axial ribs or almost spinose projections, ribs beginning at about second whorl, reaching their maximum size at whorl 4/5. Approximately 45 ribs present, running almost from suture to suture. About 16 ribs present on body whorl. Ribs of large shells connected with up to 5 spiral keels. Spiral lines present on middle and lower part of whorl height. Axial ribs and spiral cords forming reticulated pattern (Figure 8). Male (?) shells only with ribs, without spiral cords (Figure 4). Aperture ovate pyriform, adnate, angulate above, apertural margins not thickened on male shells. Umbicus narrow or absent. Shells do not show great intraspecific morphological variation but sexual dimorphism is pronounced. Operculum not preserved.



**Figures 2–9.** *Tryonia hershleri* Czaja and Estrada-Rodríguez new species. 2–3. Holotype (UJMC-130). 4. Paratype (UJMC-131). possible male shells. 5. Brown colored specimen (UJMC-132a). 6. Small specimen (UJMC-132b). 7. Apical view of shell showing spiral sculpture on teleoconch (Holotype). 8. Shell sculpture with axial ribs and spiral keels. 9. Specimen (UJMC-133). Scale bars = 1mm.

**Type Material:** Holotype (Figures 2, 3, 7), UJMC-130, 5.45 mm height  $\times$  2.63 mm width, 1.95 mm aperture length, 1.20 aperture width. Paratype 1 (Figure 4), UJMC-131, 4.05 mm height  $\times$  2.05 mm width; 1.25 mm aperture length, 1.05 aperture width. Paratype 2, UJMC-132, 5.55 mm height  $\times$  2.95 mm width; 2.00 mm aperture length, 1.25 aperture width. Alexander Czaja and José Luis Estrada-Rodríguez coll., 2013. All from type locality.

**Type Locality:** Late Pleistocene gravel deposits, Acatita Valley, west side of the road to Laguna del Rey, 8 km north of Charcos de Risa, Coahuila, Mexico, 26°16'53.77" N, 103°4'25.96" W.

**Stratum Typicum:** Late Pleistocene.

**Material Examined:** 320 specimens from the type locality.

**Etymology:** The new species is named in honor of Dr. Robert Hershler, Smithsonian Institution, for his investigations on the genus *Tryonia*.

**Geographic distribution:** So far only from the Paleo-Lake *Irritila*, Coahuila, Mexico.

**Taxonomic Remarks:** *Tryonia hershleri* new species shows morphological resemblance with species of the genus with similar shell sculpture (Figures 11–15). We include in this informal group the following fossil species:

- T. spiralistriata* Wesselingh
- T. guatemalensis* Wesselingh
- T. vivasi* Wesselingh and Macsotay
- T. nuttalli* Wesselingh
- T. scalaroides tuberculata* (de Greve)
- T. scalaroides scalaroides* (Etheridge)

The only living members of this informal *Clathrata*-group are the type species *T. clathrata* Stimpson from Nevada, United States, and *T. exigua* (Morelet) from Lake Péten Itza, Guatemala.

The species in this group have axial ribs similar to *T. hershleri* new species, but the most similar is *T. vivasi* from the Cumaca Formation, Middle Miocene of



**Figure 10.** Drawing of *Tryonia hershleri* Czaja and Estrada-Rodríguez new species (Drawing of Fernando Hernandez).

Venezuela. This South American fossil species have spiral sculpture very similar to that of *T. hershleri* new species (Figure 12). The difference is that, while *T. vivasi* has up to 8 fine spiral lines, the new species from Coahuila develops 2–4 coarse spiral cords. The aperture height in relation to the height of the shell in *T. hershleri*

new species is larger than in *T. vivasi*, but the most significant difference between these two species is their size. The smallest specimens of *T. vivasi* are 6.5 mm long, the longest shells of *T. hershleri* new species measure 5.6 mm.

Shells of *Tryonia scalaroides tuberculata* Wesselingh from the Miocene Pebas Formation of Peruvian Amazonia also have spiral sculpture but only two cords on each whorl and three on the body whorl (Figure 13). Furthermore, this Amazonian species differs from *T. hershleri* new species by having a different general shape (weakly convex whorls) and one or two more whorls.

Other members of the *Clathrata*-group such as *T. spiralistriata* Wesselingh, *T. clathrata* Stimpson and *T. scalaroides scalaroides* (Etheridge) lack the characteristic keels (or have them very poorly developed) on the whorls and therefore the general pattern of the sculpture is different (Figures 11, 14, 15).

***Tryonia pseudocircumstriata* new species**  
(Figures 17–27, Table 2)

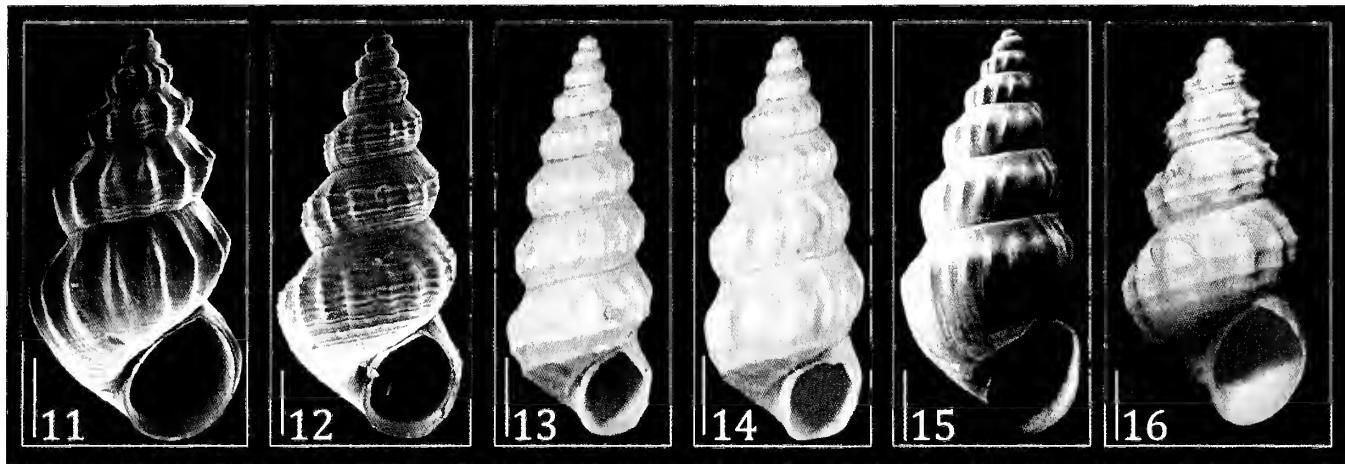
**Diagnosis:** Shell medium- to large-sized, eonical, aperture ovate, distinguished from congeners by different ornamentation of the whorls (regularly spaced spiral lirae between sutures).

**Description:** Shell up to 6.5 mm high and 1.61–2.33 mm wide (shell measurements in Table 2), elongate to conic with 5.25–7.00 very weak convex whorls. Protoconch smooth (Figure 21). Teleoconch sculptured with more or less regularly spaced spiral lirae between sutures, ranging in number from 5–7 on third whorl to 12 on body whorl; last three whorls with weak collabral ribs that cross spiral sculpture. Aperture ovate-pyriform and angulate above, lip thin, adnate. Shell imperforate or narrowly umbilicate. Shells white (typical for Pleistocene material), original coloring and operculum not preserved.

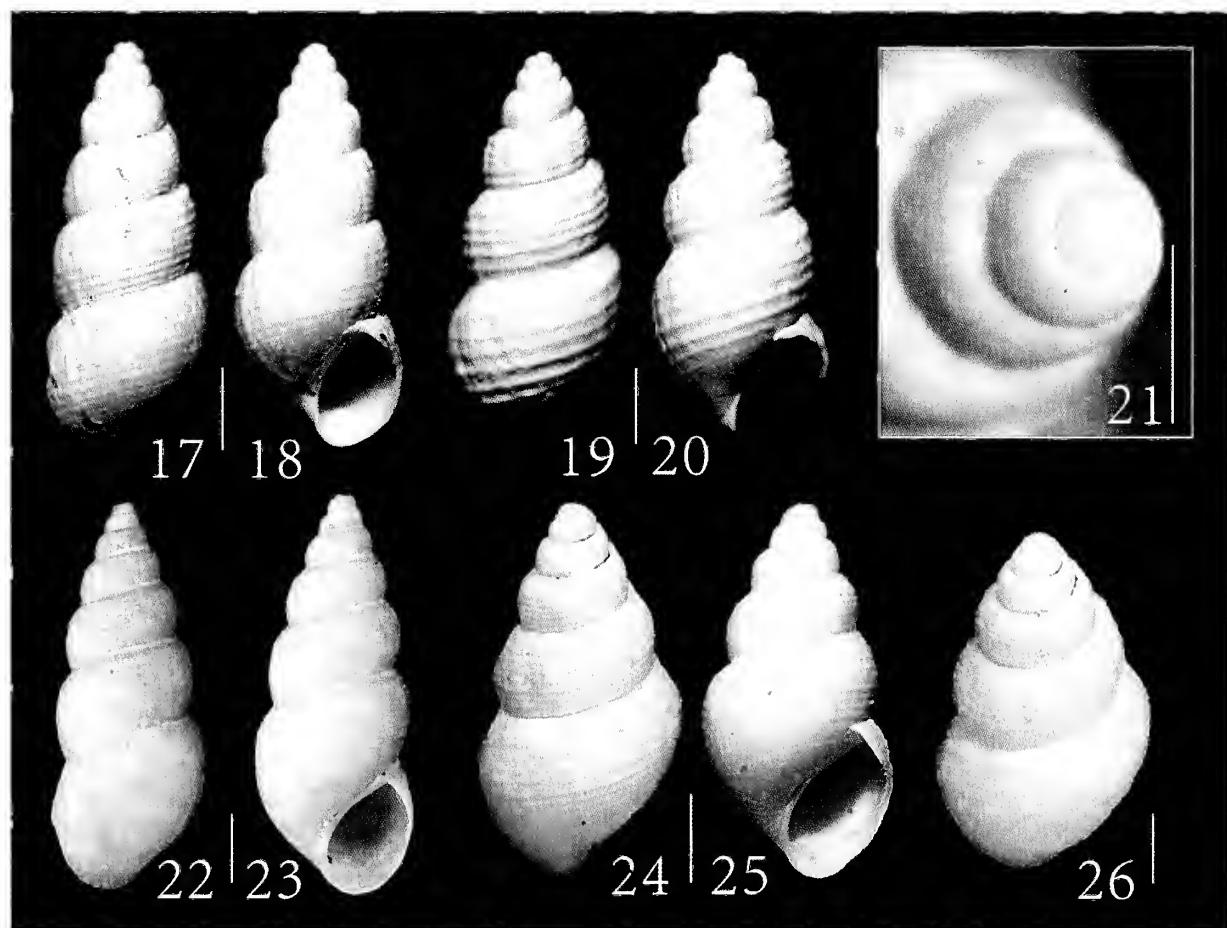
**Type Material:** Holotype (Figure 17, 18), UJMC-143, 5.05 mm height × 2.05 mm width; 1.25 mm aperture length, 1.05 aperture width; Paratype 1 (Figures 19, 20), UJMC-144, 5.15 mm height × 1.95 mm width; 1.30 mm aperture length, 1.05 aperture width; Paratype 2 (Figures 22, 23), UJMC-145, 4.95 mm height × 1.80 mm width; 1.25 mm aperture length, 1.05 aperture width. Alexander Czaja and José Luis Estrada-Rodríguez coll., 2013. All from type locality.

**Table 1.** *Tryonia hershleri* new species, shell measurements (in mm). Symbols used are:  $\bar{x}$  = mean; SD = standard deviation; N = sample size.

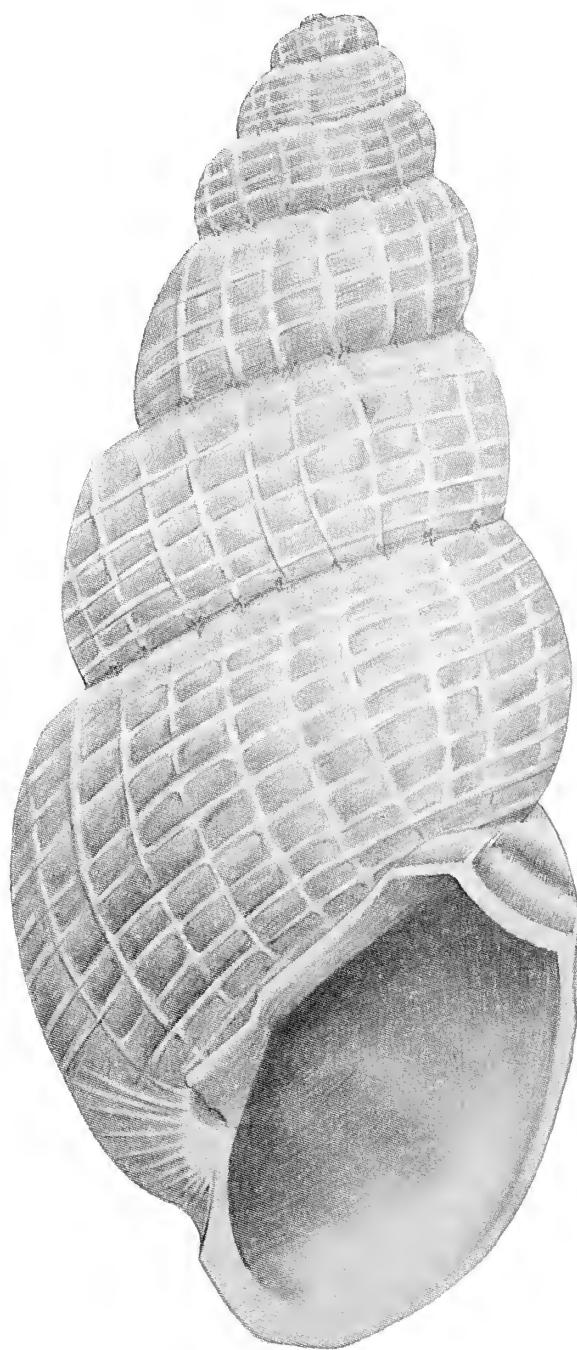
Specimen	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	$\bar{x}$	SD	N		
<b>Length</b>	5.05	4.52	3.94	5.03	4.38	4.01	3.61	3.62	4.01	3.65	4.19	4.28	4.81	4.61	4.32	3.92	5.21	3.61	4.01	4.39	4.26	1.360	20		
<b>Width</b>	2.20	2.25	1.99	2.23	2.31	2.12	2.03	2.02	2.10	1.97	2.12	2.29	2.60	2.51	2.33	2.03	2.39	1.87	1.99	2.20	2.18	0.190	20		
<b>No. whorls</b>	5.50	5.25	5.25	6.25	5.25	5.00	5.00	4.75	5.25	5.00	5.25	5.00	5.25	5.00	5.25	5.00	6.00	5.25	6.25	5.00	5.00	5.25	5.29	0.416	20



**Figures 11–16.** Comparison of sculptured *Tryonia* species. **11.** *Tryonia spiralistriata* Wesselingh and Macsotay (from Wesselingh and Macsotay, 2006, fig. 4b, reprinted with author's permission). **12.** *Tryonia vivasi* Wesselingh and Macsotay (from Wesselingh and Macsotay, 2006, fig. 3a, reprinted with author's permission). **13.** *Tryonia scalarioides tuberculata* (de Greve) Wesselingh (from Wesselingh, 2006, Fig. 27b, reprinted with author's permission). **14.** *Tryonia scalarioides scalarioides* (Etheridge) Wesselingh (from Wesselingh, 2006, Fig. 24b, reprinted with author's permission). **15.** *Tryonia clathrata* Stimpson (from Hershler, 2001, fig. 4E, reprinted with author's permission). **16.** *Tryonia hershleri* new species Scale bars = 1mm.



**Figures 17–26.** *Tryonia pseudocircumstriata* Czaja and Estrada-Rodríguez new species. **17–18.** Holotype (UJMC-143). **19–20.** Paratype 1 (UJMC-144). **21.** Apical view of shell showing spiral sculpture on teleoconch (Holotype). **22–23.** Paratype 2 (UJMC-145), smooth specimen. **24–26.** Width specimen (UJMC 146). Scale bars = 1mm.



**Figure 27.** Drawing of *Tryonia pseudocircumstriata* Czaja and Estrada-Rodríguez new species (Drawing of Fernando Hernandez).

**Type Locality:** Dunas Bilbao near Viesca, Coahuila, late Pleistocene,  $25^{\circ}26'17.45''$  N,  $102^{\circ}55'12.93''$  W.

**Stratum typicum:** Late Pleistocene.

**Material examined:** 85 specimens from type locality.

**Etymology:** The species name alludes to its morphological resemblance to *Tryonia circumstriata* (Leonard and Ho, 1960) from the Pleistocene of Pecos County, Texas, United States.

**Geographic Distribution:** Thus far known only from Bilbao Dunes, southern part of the Paleo-Lake *Irritila*, Coahuila, Mexico.

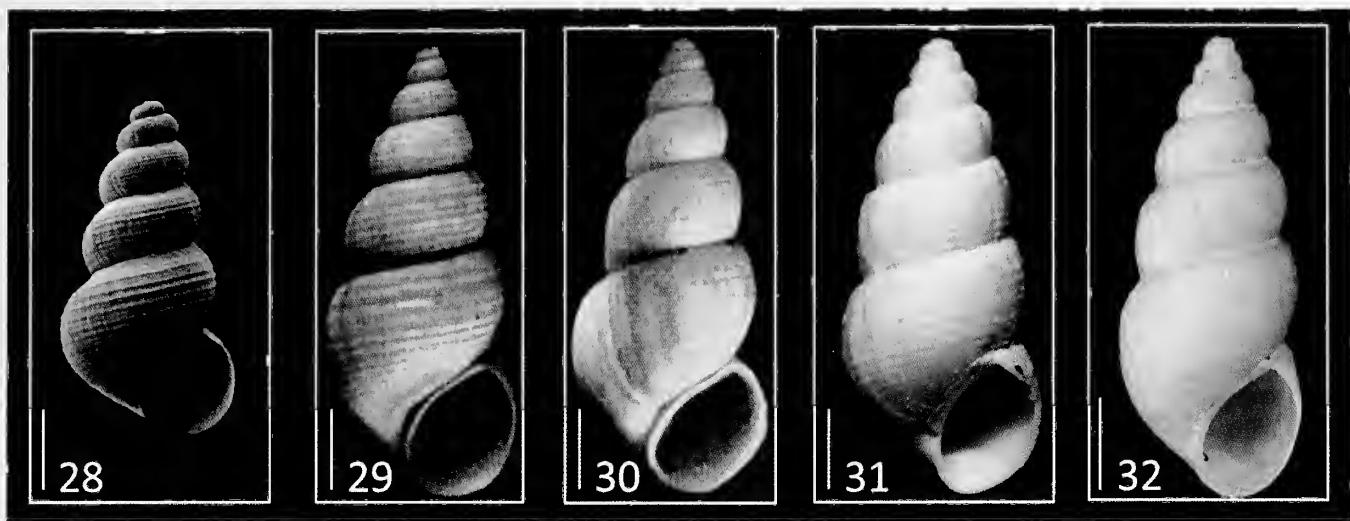
**Taxonomic Remarks:** The most characteristic feature of this new species is its teleoconch with regularly spaced spiral lirae (Figure 27). *Tryonia pseudocircumstriata* new species closely resembles (as its name indicates) *T. circumstriata* from the Pecos River deposits, Texas, United States. This species was first described by Leonard and Ho (1960) based on Pleistocene material. Subsequently, in the vicinity of the Pleistocene site, a living species was found by Taylor (1987) and named *Tryonia stocktonensis* (Gonzales Spring Snail). However, Hershler and Thompson (1992) did not find difference between the fossil and Recent material and place *T. stocktonensis* in synonymy with *T. circumstriata*. However, in our opinion, the Pleistocene and recent shells from Texas are different and should not be considered as a single species. The general shape of the fossil and the recent shells is clearly different, as made evident by the different convexity of the whorls (Figures 28–30). Sutures are also different, very deeply incised in the Pleistocene shells and shallow in the recent material (Figures 28, 29). Finally, there are differences in the size of the shells that go beyond intraspecific variability. According to Taylor (1987), the recent and endemic *T. stocktonensis* have a length range of 2.34–3.67 mm, whereas the fossil shells are within the 3.7–4.9 mm range, clearly larger.

We think that these mentioned morphological differences between the Pleistocene and recent shells from Texas make it impossible to place both in the same species. We propose to use the name *Tryonia circumstriata* only for the Pleistocene material from the Pecos River and *Tryonia stocktonensis* Taylor for the Recent endemic shells of the same region.

Our Pleistocene material from Coahuila shows generally more similarities with the Pleistocene shells from

**Table 2.** *Tryonia pseudocircumstriata* new species, shell measurements (in mm). Symbols used are:  $\bar{x}$  = mean; SD = standard deviation; N = sample size.

Specimen	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	$\bar{x}$	SD	N
<b>Length</b>	4.00	5.00	4.00	3.31	4.09	4.72	4.00	3.71	4.00	4.00	4.00	5.01	4.92	4.32	4.12	4.00	3.99	4.00	5.00	4.33	4.23	0.468	20
<b>Width</b>	1.91	1.81	1.89	1.40	1.88	1.95	1.92	1.81	1.59	1.99	1.97	2.09	2.00	1.92	1.61	1.86	1.59	1.75	2.00	1.98	1.85	0.176	20
<b>No. whorls</b>	5.25	6.00	6.00	5.00	6.00	7.00	6.00	6.00	6.00	7.00	6.75	7.00	6.25	6.00	6.00	6.25	6.00	6.25	7.00	6.00	6.19	0.543	20



**Figures 28–32.** Comparison of *Tryonia pseudocircumstriata* new species with similar Pleistocene and present-day species. **28.** *Tryonia stocktonensis* Taylor, present-day endemic species from Diamond Y Draw, Pecos County, Texas (from Hershler 2001, Fig. 4H, USNM 883958, reprinted with author's permission). **29.** *Tryonia circumstriata* (Leonard and Ho) from Late Pleistocene of Pecos River deposits, Terrell County, Texas (holotype *Calipyrgula circumstriata* Leonard and Ho, 1960, Plate 12, Fig. 1, No. 11301). **30.** *Tryonia circumstriata* (Leonard and Ho) from Late Pleistocene of Pecos River deposits, Terrell County, Texas (paratype 1 *Calipyrgula circumstriata* Leonard and Ho, 1960, Plate 12, Fig. 2, No. 11302). **31.** *Tryonia pseudocircumstriata* new species, holotype (UJMC-143). **32.** *Tryonia pseudocircumstriata* new species, paratype (UJMC-145). Scale bars = 1mm.

Texas (Figures 29–32). The shells from Coahuila differ from fossil *T. circumstriata* in having only slightly convex whorls while the species from Texas have more rounded whorls. The apertures are also different: in all specimens of *T. pseudocircumstriata* new species the inner lip is always adnate to the pariental wall while specimens of *T. circumstriata* show a narrow gap between the lip and pariental wall (Figures 29–32).

#### ACKNOWLEDGMENTS

The authors are grateful to Dr. Robert Hershler, Smithsonian Institution, who first recognized that the Pleistocene specimens from Coahuila are new species of the genus *Tryonia*. Special thank goes to Dr. Heike Reise, Senckenberg Museum für Naturkunde Görlitz, Germany, for her assistance in the revision of the English text.

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# A new *Latiromitra* (Gastropoda: Ptychatractidae) from the Gulf of Mexico

Emilio F. Garcia

115 Oakcrest Dr.  
Lafayette, LA 70503 USA  
efg2112@louisiana.edu

## ABSTRACT

*Latiromitra niveobabelis* new species is described and compared with the Philippine species *Latiromitra barthelowi* (Bartsch, 1942), and with the Atlantic species *Latiromitra cryptodon* (P. Fischer, 1882), *L. aratiuncula* (Quinn, 1981), *L. meekiana* (Dall, 1889), *L. costata* (Dall, 1890) and *L. stylola* (Dall, 1927).

## INTRODUCTION

For some twenty years the Biology Department at the University of Louisiana at Lafayette (ULL), has conducted a series of cruises in the Gulf of Mexico utilizing the R/V Pelican, a ship managed by the Louisiana Universities Marine Consortium (LUMCON). The most recent cruise, one of five executed under the Gulf of Mexico Research Initiative (GoMRI), was conducted in September, 2014. The cruise sampled deep-water areas west of the Dry Tortugas. It was in this southeastern quadrant of the Gulf where an empty specimen of an unknown species of the genus *Latiromitra* was dredged.

The genus *Latiromitra* has had a controversial saga in its systematic history. Species in that genus having been placed in Buccinidae (later transferred to Costellariidae) by Thiele (1929), in Fasciolariidae and Mitridae by Dall (1889 and 1890; and 1927 respectively), in Volutidae by Weaver and Dupont (1970) and in Volutomitridae by Cernohorsky (1970). Bayer (1971: 196) noted that the species, placed in *Latiromitra*, had “a closer affinity with the family Turbinellidae”, and latter workers followed his lead. Although Quinn (1981: 72) thought it necessary to create the new genus *Cyomesus* for some members of this group, Bouchet and Warén (1985: 255) concluded that Quinn’s taxon was synonymous with *Latiromitra*. Kantor (2014) places *Latiromitra* in Ptychatractidae, and I here follow his lead. The familial placement of the genus is tentative, as this is a “taxonomically complicated group” (Kantor, personal communication, Feb. 3, 2015), very similar to some of the deep water Costellariidae.

Species assigned to the genus *Latiromitra* are relatively morphologically conservative; they are represented in the western Atlantic by five species. The new species proposed herein is known from only one empty shell; however, several of its conchological characters are quite distinct from any other *Latiromitra*.

## SYSTEMATICS

Family Ptychatractidae Stimpson, 1865

**Genus *Latiromitra* Locard, 1897**

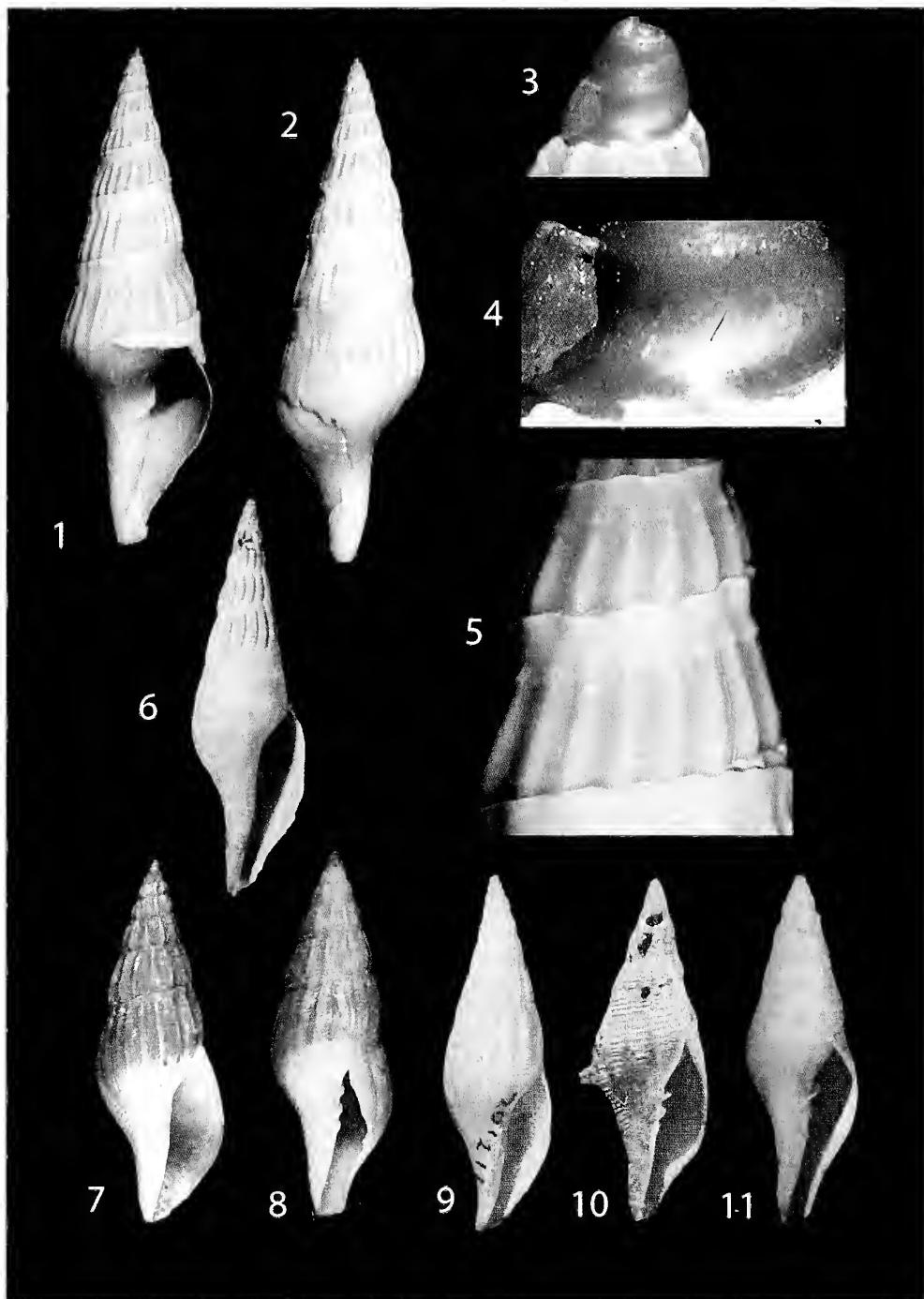
**Type Species:** *Latiromitra specialis* Locard, 1897, by monotypy.

***Latiromitra niveobabelis* new species**

(Figures 1–5)

**Diagnosis:** A milky-white, almost straight-sided, narrowly fusiform shell with a constricted subsutural band bordered posteriorly by strong, adpressed crenulations and anteriorly by a heavily nodulose spiral cord.

**Description.** Holotype 46.0 mm in length, strong, narrowly fusiform (length/width ratio 3.36); last teleoconch whorl 21.1 mm in length. Protoconch broadly conical (Figure 3), light amber in coloration, of approximately 2.5 whorls; first whorl damaged, smooth; second whorl smooth; last whorl developing weak, prosocline axial riblets on approximately last half of whorl (Figure 4); riblets growing stronger at termination of whorl. Transition to teleoconch abrupt, with a strongly prosocline transitional growth mark, a change in coloration from amber to milky-white, and a development of a round axial rib at start of teleoconch (Figures 3–4). Teleoconch of 8.5 whorls; whorls subsuturally constricted (Figure 5), only slightly convex anteriorly; last whorl strongly convex peripherally. Suture deep, heavily crenulate; crenulations strongly adpressed to earlier whorl, creating a narrow channel (Figure 5), this feature first appearing between second and third teleoconch whorls. Axial sculpture of strong, rounded ribs; ribs as wide as interspaces; 10 ribs on first



**Figures 1–10.** *Latiromitra niveobabelis* and other species for comparison. **1–5.** *Latiromitra niveobabelis* new species. Holotype, USNM 1274447, west of Dry Tortugas,  $25^{\circ}51.104' N$ ,  $84^{\circ}52.278' W$  to  $25^{\circ}49.867' N$ ,  $84^{\circ}52.400' W$ , in 1737 m, 46.0 mm. **6.** *Latiromitra barthelowi* (Bartsch, 1942). Holotype, USNM 238444, Cagayan Island, Sulu Sea, Philippines, 905 m, 27.5 mm. **7–8.** *Latiromitra cryptodon* (P. Fiseher, 1882). Syntype, off Morocco,  $33^{\circ}29' N$ ,  $09^{\circ}38' W$ , 1900 m, 30 mm, photo by M. Caballer (MHN). Project : E-Recolnat ANR-11-INBS-0004. **9.** *Teramachia chaunax* Bayer, 1971. Holotype, USNM 701216 west of St. Lucia,  $13^{\circ}45.5' N$ ,  $61^{\circ}05.7' W$ , 201–589 m, 28 mm, photo by J.F. Quinn, Jr. **10.** *Latiromitra aratiuncula* (Quinn, 1981). Holotype, USNM 784594, off Anguilla,  $18^{\circ}26.4' N$ ,  $63^{\circ}63'12.6' W$ , 430 m, 29 mm (photo credit J. F. Quinn). **11.** *Latiromitra meekeana* (Dall, 1889). Lectotype, USNM 86970, off Morro Light, Havana, Cuba, 732 m, 15.5 mm, photo by J.F. Quinn, Jr.

whorl, gradually increasing to approximately 21 on penultimate whorl and 24 on last whorl; a few, weak secondary axial riblets sporadically appearing on last whorls; axial sculpture diminishing towards anterior end of last whorl, completely disappearing at siphonal canal. Spiral sculpture of two strongly nodulose cords on first whorl; first cord at suture; second cord just below; sutural cord later creating a narrow, heavily crenulate channel (Figure 5); both spiral cords delimiting a constricted band subsuturally, of approximately 2 mm in width on last whorl; weak, secondary spiral threads covering the surface of the shell, crossing over axial ornamentation creating subtle nodes; approximately 20 stronger spiral cords developing at anterior end of last whorl. Aperture narrowly elongate, approximately 19 mm in length; outer lip thin; parietal wall with three oblique, well-developed lamelliform plaits; posterior plait strongest. Shell milky-white, with a faint yellowish coloration showing at, and restricted to, the subsutural band.

**Type Material:** Holotype USNM 1274447, length 46.0 mm, width 13.7 mm.

**Type Locality:** West of Dry Tortugas, USA (25°51.104' N, 84°52.278' W to 25°49.867' N, 84°52.400' W, in 1737 m (GoMRI-V, station 10).

**Distribution:** Known only from the type locality.

**Habitat:** *Latiromitra niveobabelis*, like other congeners, is a deep-water species. It was collected in a mud bottom with rubble. Other notable species dredged in the same haul were *Theta chariessa* (Dall, 1889) and *Stellatoma antonia* (Dall, 1889).

**Etymology:** A combination from the Latin adjective *niveo*, and the biblical tower of Babel; referring to the white, tower-like shape of the shell.

**Remarks:** The tapered profile of the new species is most similar to the western Pacific *Latiromitra barthelowi* (Bartsch, 1942), but the latter has a paucispiral protoconch, weak axial ornamentation after the fourth whorl and, of the three columellar plaits, the abapical one is weak to absent (Bouchet and Kantor, 2000: 13). The new species is also similar to *Latiromitra cryptodon* (P. Fischer, 1882) (Figures 6–9), an amphiatlantic species ranging, in the western Atlantic, from the Bahamas to Brazil (Rosenberg, 2009). This species differs from *Latiromitra niveobabelis* in having a different protoconch sculpture (see Bouchet and Kantor, 2000: 10, fig. 5K), in having fewer teleoconch whorls, in lacking the well-developed, constricted subsutural band (compare Figures 5 and 6), in having weaker sutural crenulations, and in having different coloration. Caribbean specimens of *Teramachia chaunax* F.M. Bayer, 1971 (Figure 9), a junior synonym of *L. cryptodon*, have a more slender profile than the NE Atlantic and Brazilian specimens of *L. cryptodon*; how-

ever, they are otherwise undistinguishable from the type material of the latter (Bouchet and Kantor, 2000: 10).

*Latiromitra aratiuncula* (Quinn, 1981) (Figure 10), from off Anguilla, lacks the constricted subsutural band, has coarser shell ornamentation with stronger spiral cords, and fewer axial ribs. *Latiromitra meekeana* (Dall, 1889) (Figure 11), the only *Latiromitra* recorded from the Gulf of Mexico (Rosenberg et al. 2009), has a paucispiral protoconch of 1.3 whorls, is pale waxen or brownish in coloration, lacks the constricted subsutural band and is almost smooth after the fourth whorl. *Latiromitra costata* (Dall, 1890) is much smaller, has strongly convex whorls, and fewer, stronger axial ribs. *Latiromitra styliola* (Dall, 1927), which has tentatively been placed in *Latiromitra* by Bouchet and Kantor (2000) has a protoconch of 1.5 whorls, has 5 teleoconch whorls and reaches 11 mm in length.

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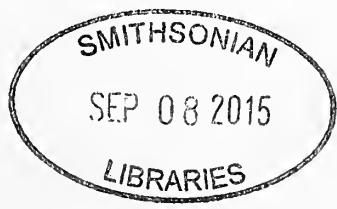
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# THE NAUTILUS



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# A revision of the western Atlantic Ocean genus *Engina* with notes on *Hesperisternia* (Gastropoda: Buccinidae: Pisaniinae)

**G. Thomas Watters**

Department of Evolution, Ecology, and Organismal Biology  
The Ohio State University  
Columbus, Ohio 43212 USA  
watters.1@osu.edu

**Koen Fraussen**

Leuvensestraat 25  
B-3200 Aarschot, BELGIUM  
koen.fraussen@skynet.be

## ABSTRACT

The western Atlantic Ocean members of the genus *Engina* Gray, 1839, are reviewed. The following taxa are recognized: *E. annae* new species, *E. corinnae* Crovo, 1974, *E. demani* de Jong and Coomans, 1988, *E. goncalvesi* Coltro, 2005, *E. itzamnai* (Watters, 2009), *E. lignaea* new species, *E. permixta* new species, *E. turbinella* (Kiener, 1836), and *E. williamsae* new species. Distributional notes are also given for *Hesperisternia karinae* (Nowell-Usticke, 1959).

## INTRODUCTION

The systematics of *Engina* is confusing as the genus has a complicated taxonomic history. Early species were described in the genus *Voluta* by Linnaeus (1758) and Wood (1828), in *Buccinum* by Lamarck (1822), in *Columbella* by Sowerby (1832) and Duclos (1840), and in *Purpura* by Kiener (1836). Even after the description of the genus *Engina* in 1839 species continued to be described in *Buccinum* by Küster (1858), in *Pollia* by Dunker (1860), in *Tritonidea* by E.A. Smith (1884), and other genera, but especially in *Ricinula* by Reeve (1846). In addition, aside from actual buccinid species, members of other families (Muricidae, Columbellidae, etc.) also were included in those genera and, for the simple reason that many of those small shells look similar, it was not until Pease (1860), Melvill (1893; 1894a; 1984b; 1895) and Melvill and Standen (1895) that the name *Engina* was finally used in publications. Tryon (1883) and Pace (1902) considered *Engina* to be a columbellid genus.

*Engina* was introduced by J.E. Gray in *The Zoology of Captain Beechey's Voyage*. In the Introduction to this publication, Beechey (in Gray, 1839: vii) stated that “I wish I could with sincerity have included with the above-mentioned [acknowledged] names that of Mr. J. E. Gray, who undertook to describe the shells, but the publication has suffered so much by delay in consequence of his having been connected with it, that it is a matter of the

greatest regret to me that I ever acceded to his offer to engage in it... [This eight year delay] has been occasioned entirely by Mr. Gray's failing to furnish his part in spite of every intercession from myself and others.” Beechey continued in this vein for another page. Gray had listed two species in the genus, neither collected during the voyage, both new but unillustrated, and did not select a type of the genus. Both species, *E. zonata* and *E. elegans*, have been the subject of debate due not only to Gray's lack of illustration, but to his apparent gross mis-measurement of the specimens, giving lengths 10 times greater than the actual shells, and the vague type localities for both: “Atlantic Ocean.” Gray subsequently (1847) picked *E. zonata* as the type while misspelling *Engina* as *Enzina* (also misspelled in 1842).

Landau and Vermeij (2012) considered *Engina* to be a group of intertidal and shallow subtidal species. However, most of the species considered here occur in significantly deeper water; live individuals often occur in depths > 45 m, some to hundreds of meters. Of the western Atlantic species only *E. turbinella* truly occurs predominately in shallow water. Most species are associated with rocky reefs or coral debris, whereas some occur in caves. As with many other gastropod genera, *Engina* harbors a number of species that are common or even abundant whereas several species are quite rare and rarely represented in collections.

The type species of *Engina*, *E. turbinella*, is a member of the shallow water fauna and therefore shows the shell characteristics that are representative of *Engina* species from that fauna. Most, or all, shallow water *Engina* species bear the characteristic radially oriented lirae on the columella that are seen in the type species. Nevertheless many *Engina* live in deeper water and differ slightly or even radically from the shallow water morphs. In deeper water (ca. > 45 m) species may lack these radially orientated lirae on the parietal part. The shallow and deep water morphs are not well separated and it remains a question of whether this is the result of variability (the opinion followed in the present paper) or rather that our current concept of *Engina* is based on a heterogeneous group (the result of the presence of unrecognized genera).

In the present paper we regard *Engina* in a rather conservative way, grouping together the shallow and deep-water species. Further study may indicate that additional genera are required.

The type species of *Engina*, together with the species discussed in the present paper, are members of the Atlantic Ocean fauna. A much larger number of *Engina* species is known from the Indo-West Pacific and eastern Pacific oceans. We believe that both the Atlantic and Indo-West Pacific species belong to the same genus, as so many other genera do, and we see no reason to split *Engina* into distinct groups based on geographical distribution.

Apart from a higher biodiversity in the Indian and Pacific oceans, the morphological variability within the genus is also higher there than in the Atlantic Ocean. Slender, fusiform shells are a frequent shape in the Indo-West Pacific Ocean whereas none are known to us from the Atlantic Ocean. Those slender species have a different appearance than do broad ones and tend to live in deeper water; nevertheless we regard them as included within the variability of the genus. "Typical" species have radiating columellar riblets. In some species those are well expressed and striking but other species show this sculpture only under magnification.

Many Western Atlantic Ocean species have eastern Pacific Ocean cognates. Atlantic taxa such as *E. turbinella* and *E. permixta* closely resemble Pacific species such as *E. mantensis* Bartsch, 1928, *E. maura* (Sowerby, 1832), and *E. tabogaensis* Bartsch, 1931. The Pacific *E. pulchra* (Reeve, 1846) is particularly close to the Atlantic *E. demani*. But taxa such as the Pacific *E. fusiformis* Stearns, 1894, and the Atlantic *E. goncalvesi* do not have similar cognates. Vermeij (2006) recognized the close relationship between the Pacific *Hesperisternia jugosa* (Adams, 1852), previously considered an *Engina* (Keen, 1971), *H. lauta* (Reeve, 1846), previously considered a *Cantharus* (Keen, 1971), and the Atlantic *H. karinae* (reviewed here).

A fossil record for *Engina* was nearly lacking until Landau and Vermeij (2012) reviewed the western Atlantic taxa. They identified *Engina cantaurana* Landau and Vermeij (2012) from the early Miocene of Venezuela as the oldest known member of the genus but did not believe it was closely related to any Recent species. They found that *Engina latior* Landau and Vermeij (2012) from the early Pliocene of the Dominican Republic, *E. moinensis* Landau and Vermeij (2012) from the early Pleistocene of Panamá, and *E. floridana* Olsson and Harbison, 1953, from the early Pleistocene of Florida, were more similar to Recent species. *Engina moinensis*, in particular, is very similar to the two rare, deep-water Yucatán taxa discussed here: *E. itzamnai* and *E. lignea*. The extant *E. turbinella* was recognized from the middle Miocene of Panamá (Woodring, 1973) and the late Pleistocene of the Dominican Republic (Landau and Vermeij, 2012).

Spiral and axial sculpture are features with a remarkably low degree of infraspecific variability within the genus *Engina*. Variability in pattern and color, to the contrary, is remarkably high for some *Engina*. While most species are moderately uniform in these character-

istics, without displaying much variation in pattern or color, a number of other species are strikingly variable. This was first discussed concerning a Philippine species (Fraussen and Chino, 2012); in the present paper we show a similar level of variability in at least two species.

As remarked by Cernohorsky (1975) and Faber (2007), *Engina cumingiana* Melvill, 1895, from "St. Thomas" appears to be a mislabeled, but as yet unidentified, species. It is not similar to any of the species covered here. *Engina willemseae* de Jong and Coomans (1988) was transferred to *Anna* by Watters (2009) and to *Ameranna* by Landau and Vermeij (2012). *Engina slootsi* de Jong and Coomans (1988) is *Habromorula biconica* (Blainville, 1832) (Muricidae) from the Pacific Ocean (*fide* Houart, 1994).

## MATERIALS AND METHODS

Length is measured from the tip of the apex to the end of the siphonal canal. Width is measured as the maximum dimension in a plane with facing the aperture. Spiral sculpture is counted from the suture to the end of the siphonal canal. Descriptions of apertural features are based on the terminology adopted by Landau and Vermeij (2012). Lirae counts within the outer lip may include bifurcating lirations. The number of whorls was determined using the 1 D method of Van Osselaer (1999). Locality information, aside from type locality designations, may be amplified from the original label for clarification. Given the generalized nature of most label information, no attempt has been made to georeference sites that did not originally include coordinates. Dimensions in captions refer to shell length. Numbers in ( ) following catalog numbers indicate the number of specimens in the lot.

Abbreviations used in the text are: AMNH: American Museum of Natural History, New York City, New York, USA; BMSM: Bailey-Matthews National Shell Museum, Sanibel, Florida, USA; NHMUK: Natural History Museum, London, UK; EFG: Collection of Emilio F. García, Lafayette, Louisiana, USA; GTW: Collection of G. Thomas Watters, Columbus, Ohio, USA; HGL: Collection of Harry G. Lee, Jacksonville, Florida, USA; KF: Collection of Koen Fraussen, Aarschot, Belgium; MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MW: Collection of Margaret Williams, Tallevast, Florida, USA; OSUM: Ohio State University Museum of Biological Diversity, Columbus, Ohio, USA; PRI: Paleontology Research Institute, Ithaca, New York, USA; UF: Florida Museum of Natural History, Gainesville, Florida, USA; ZMA: Zoölogisch Museum, Amsterdam, The Netherlands.

## SYSTEMATICS

Family Buccinidae Rafinesque, 1815  
Subfamily Pisaniinae Gray, 1857

### Genus *Engina* Gray, 1839

*Engina* Gray, 1839: 112–113.

**Type Species:** *Engina zonata* Gray, 1839, by subsequent designation of Gray (1847) [= *Purpura turbinella* Kiener, 1835, see Orr (1962)].

**Discussion:** The morphological limits and unique features of *Engina* have not been easy to define. Cernohorsky (1975: 176) characterized the genus by “the radially oriented lirae [which] are found only in species of *Engina*,” a feature that Landau and Vermeij (2012) nevertheless noted was not present in all *Engina*. Landau and Vermeij (2012: 121) defined the genus by “a shell with a narrow, strongly denticulate aperture and the presence of distinct columellar folds” but admitted that “not all species... conform to this characterization.” Definitive differences between *Engina* and *Hesperisternia* appear to be particularly ambiguous. Vermeij (2009) noted that some *Hesperisternia* had shell sculpture and apertural features that were convergent with *Engina*. Watters (2009) placed *E. janowskyi* and his species *itzamnai* in *Hesperisternia*; Landau and Vermeij (2012) reallocated them to *Engina*. That reallocation is followed here and we confirm the importance of the presence of internal lirae that extend far into the aperture as an important feature to distinguish *Hesperisternia* from *Engina*.

Adding to the problems of identifying the western Atlantic species is the great variability seen in conchological features. Coloration, sculpture, degree of elongation, and apertural features are highly plastic. Given a small number of specimens it is easy to conclude that numerous taxa are involved. However, when larger lots are studied it is apparent that there are intergrades that unite such disparate forms.

The species recognized in this review are presented in alphabetical order, including the type species of *Engina*, *E. turbinella* (Kiener, 1835).

#### *Engina annae* new species (Figures 1–4, 13)

*Engina* species.—Lee, 2009: 108, fig. 518a.

**Description (based on 2 adult specimens):** Larger adult specimen seen, 15.6 mm in length (holotype); smaller specimen seen, 12.9 mm in length; holotype 15.6 mm length × 8.9 mm width. Shell biconic; spire ca. 50% total length. Protoconch minute, of 1.5 smooth, pale tan whorls. Teleoconch of 5.5 whorls, demarcated from protoconch. Teleoconch sculpture of 9–10 primary rounded spiral cords, between the suture and the anterior limit of the siphonal canal, three grouped at periphery; concave or flat, wide subsutural slope with a single thin primary cord. Secondary microscopic spiral threads between primary spiral sculpture. Primary axial sculpture of broad, low, rounded ribs, very weak on subsutural slope; 10 ribs on penultimate whorl, 10 on final whorl. Extremely fine secondary wrinkles occur between axial ribs. Terminal varix weak. Aperture oval, elongate. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 5–7 denticles, decreasing in size from posterior to ante-

rior, the posterior-most two with a tendency to be weakly fused. The thin rib that projects deep into the aperture and delimits the siphonal canal found in other species is weak. Five radial lirae present at posterior end, barely distinct from columellar folds. Anterior to these are 6–8 columellar folds irregular, some lirate, others pustulose. One or more denticles extending deep into aperture, forming an interior ledge to columella. Parietal lip erect for most of its length. Siphonal canal short, open. Color gray with a tan subsutural band; axial ribs dark brown, often with a white adapertural face forming a series of dark and light spots; there is a continuous, white spiral band just below the periphery. Aperture tan with white teeth. Operculum, radula, and anatomy unknown.

**Holotype:** UF 479323 (ex Mark Johnson coll. 0142).

**Type Locality:** 33 m., 48 km off Masonboro Inlet, Wrightsville Beach, New Hanover Co., North Carolina, USA.

**Paratype(s):** Charlotte Thorpe coll. (1), Amberjack Hole, E of Mayport, Duval Co., Florida, USA.

**Distribution:** Only known from offshore of southernmost North Carolina and northeast-most Florida. We assume it occurs off the intervening South Carolina and Georgia coasts as well.

**Habitat:** The holotype was a crabbed specimen from 33 m, collected on sandy rubble near rocky outcrops with sponges.

**Shell Variation:** The known specimens are remarkably uniform in sculpture and coloration.

**Etymology:** Named for Ann Johnson, mother of the collector of the holotype, Mark Johnson.

**Comparison with Other Species:** The peculiar coloration of dark brown and white spots on a gray background has not been found in any other western Atlantic species. See Table 1 for a comparison with other species.

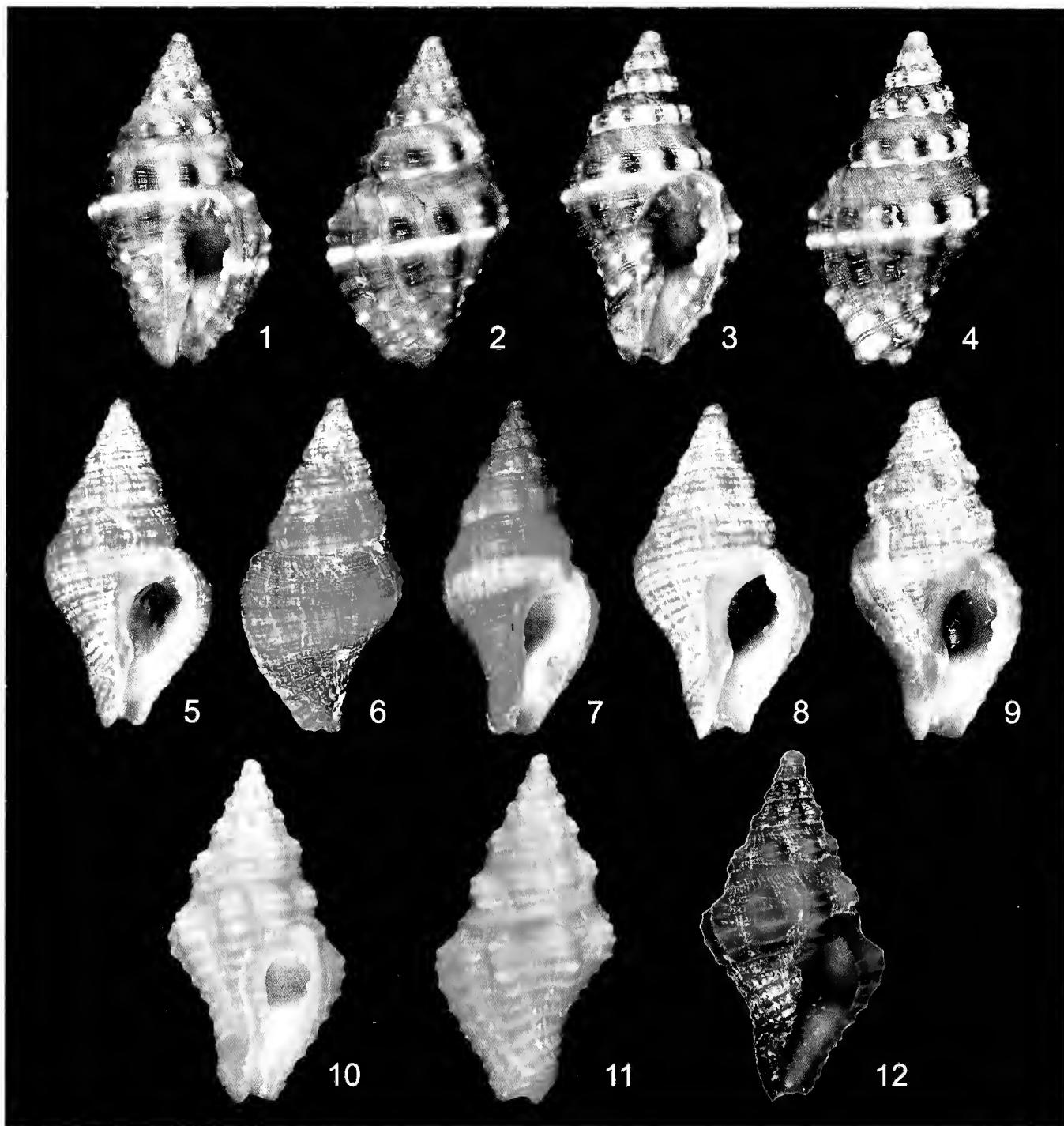
**Discussion:** This extremely rare species is the northernmost member of *Engina* in the western Atlantic Ocean. Like most of the species discussed here, it is an offshore species seldom encountered. It was first recognized as distinct by Lee (2009).

#### *Engina corinnae* Crovo, 1974 (Figures 14–33, 34)

*Engina corinnae* Crovo, 1974: 30, figs. 1–3; Abbott, 1974: 217, fig. 2398; Odé, 1983: 60; Kaicher, 1986: card 4405; Landau and Vermeij, 2012: 122, 123, 126; Petuch, 2013: 202.

*Engina corinnae* of authors, *non* Crovo, 1971. — Lee, 2009: 108, fig. 518.

**Description (based on 38 adult specimens):** Largest adult specimen, 14.8 mm in length; smallest specimen, 9.2 mm in length. Shell biconic; spire ca. 50% total



**Figures 1–12.** *Engina* species. **1–4.** *Engina annae* new species. **1–2.** Holotype, UF 47923, 15.7 mm. **3–4.** Paratype Charlotte Thorpe coll., Amberjack Hole, E of Mayport, Duval Co., Florida, 12.9 mm. **5–9.** *Engina goncalvesi* Coltro, 2005. **5–6.** GTW 12447a, 40–50 m, in cave, off Arraial do Cabo, Rio de Janeiro State, Brazil, 11.3 mm. **7.** GTW 12447b, 150–160 m, off Cabo Frio, Rio de Janeiro State, Brazil, 13.9 mm. **8.** HGL, 40–44 m, in cave, off Arraial do Cabo, Rio de Janeiro State, Brazil, 9.5 mm. **9.** GTW 12479a, 40–50 m, in cave, off Arraial do Cabo, Rio de Janeiro State, Brazil, 11.3 mm. **10–11.** *Engina linea* new species. **10–11.** Holotype, UF 479325, 14.3 mm. **12.** Paratype, BMSM 76001, 50–55 m, 146 km WSW of Arrecife Alacrán, Campeche Bank, Campeche State, Mexico, 11.5 mm.

length. Protoconch minute, of 1.5 smooth whorls, white with tan patches or bands. Teleoconch of 4.75–5.25 whorls, demarcated from protoconch. Teleoconch sculpture of 9–12 (mode=11) primary sharp spiral cords

between the suture and the anterior limit of the siphonal canal, weakest on concave or flat subsutural slope; elsewhere of uniform strength except that spiral cords on siphonal canal are slightly stronger. Secondary microscopic



**Figure 13.** Distribution of *Engina annae* new species (◎), *Engina goncalvesi* Coltro, 2005 (●), *Engina lignaea* new species (●), and *Engina williamsae* new species (★).

spiral threads between primary spiral sculpture. Primary axial sculpture of broad, low ribs, absent from subsutural slope; 7–10 (mode=9) ribs on penultimate whorl, 6–13 (mode=10) on last whorl, most pronounced at periphery. Coarse secondary wrinkles occur between axial ribs which may be lamellate. Terminal varix weak. Aperture oval, elongate. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 6–8 (mode=6) denticles. The thin rib that projects deep into the aperture and delimits the siphonal canal found in other species is weak but always present. 2–5 (mode=3) radial lirae present at posterior end, weak and irregular, not distinct from columellar folds. Anterior to these are 4–7 (mode=6) semi-lirate columellar folds irregular, often limited to edge of parietal wall, weakest or absent on middle of columella. First or second anterior denticle often extending deep into aperture forming

an interior ledge to columella. Parietal lip erect for most of its length. Siphonal canal short, open. Color white or pale tan with brown blotches, darkest between axial ribs, particularly on the spire, with a wide, white subperipheral band; usually two fine, dark threads posterior to this band on the final whorl. Aperture white, faint tan, or mauve, darkest at anterior end. Operculum rounded, leaf-shaped, yellow with brown central radius. Radula and anatomy unknown.

**Holotype:** MCZ 277496.

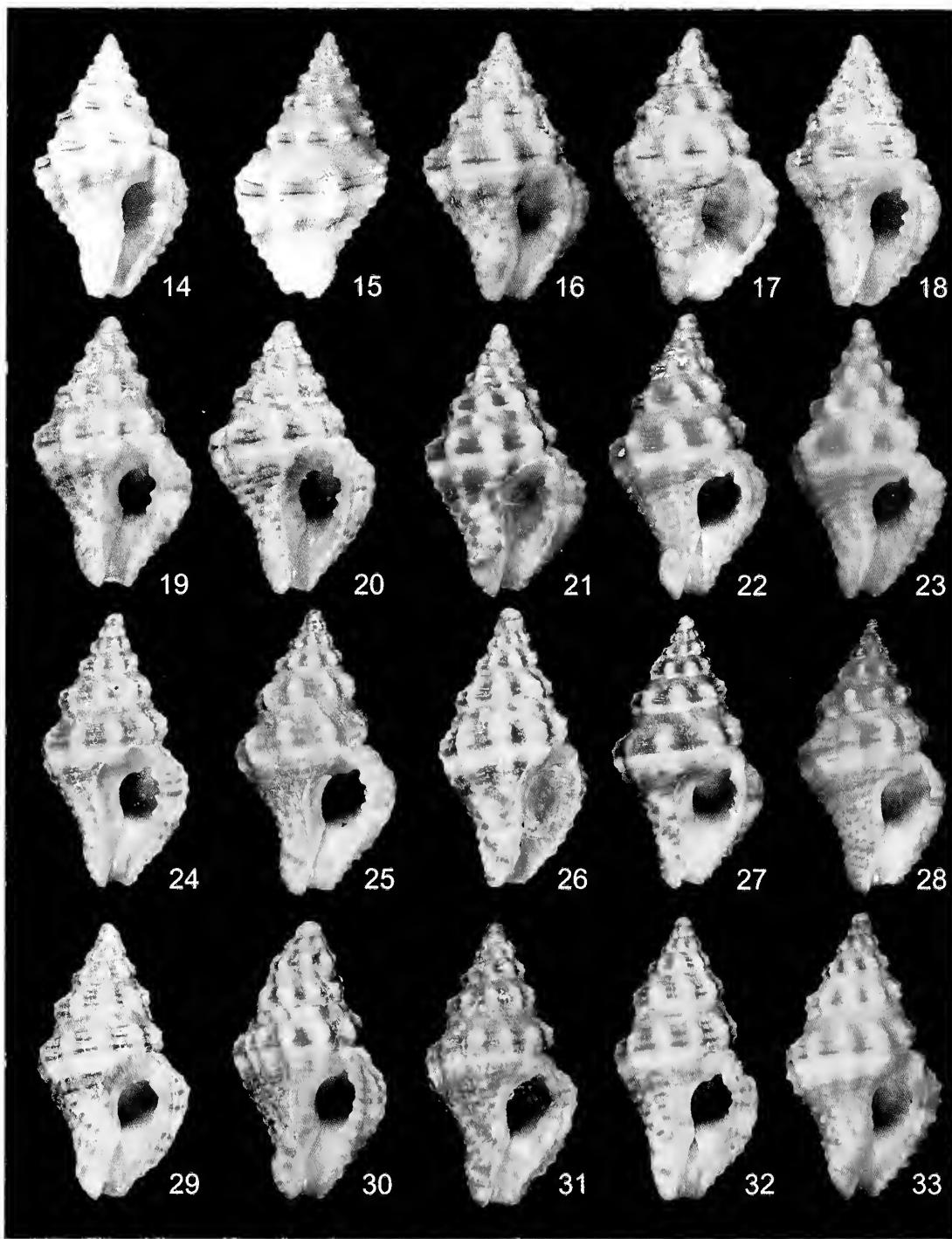
**Type Locality:** Off Boynton Beach, Palm Beach County, Florida, USA, 30° 00' N, -79° 57'30" W. Depth unknown.

**Paratype(s):** MCZ 277497 (unstated number of specimens); PRI 28273 (1); all from the type locality.

**Other Material Examined (124 specimens):** East Florida: MW (1), 27 m, off eastern Florida; MW (1), 34 m, off Mayport, Duval Co.; MW (1), HGL (6), 30–46 m, off St. Augustine, St. Johns Co.; UF 35241 (1), 18 m, off Boynton Beach, Palm Beach Co.; UF 128074 (66), 27 m, off Boynton Beach, Palm Beach Co.; UF 128051 (3), 27–38 m, off Boynton Beach, Palm Beach Co.; EFG 9553 (2), 38–43 m, off Boynton Beach, Palm Beach Co.; HGL (1), Boynton Beach, Palm Beach Co.; UF 352841 (1), 18 m, off Boynton Beach, Palm Beach Co., Florida; UF 122778 (7), 107 m, off Boynton Inlet, Palm Beach Co.; UF 126244 (1), 26 m, off Boynton Inlet, Palm Beach Co.; UF 228793 (6), 73 m, off Palm Beach, Palm Beach Co.; UF 127142 (1), off Palm Beach, Palm Beach Co.; UF 229058 (1), 55–73 m, off Palm Beach, Palm Beach Co.; UF 262537 (2), 91–152 m, off Palm Beach, Palm Beach Co.; UF 126241 (7), 37 m, off Palm Beach, Palm Beach Co.; UF 228990 (2), 37–46 m, off Palm Beach Inlet, Palm Beach Co.; UF 250037 (2), 37–55 m, Dodge Estate to inlet, Palm Beach Co.; EFG 13895 (1), 30 m, off West Palm Beach, Palm Beach Co.; HGL (3), 183–213 m, off Looe Key, Monroe Co. West Florida: EFG 28347 (1), 61 m, off Egmont Key, Hillsborough Co.; MW (1), HGL (5), 27 m, off Panama City, Bay Co.; MW (2), 6.4 km off

**Table 1.** Shell characteristics of *Engina* and *Hesperisternia*. Numbers in ( ) are modes except for length, which are averages; \* – no mode.

Taxon	Number of Radial Lirae	Number of Columellar folds	Number of Outer Lip Denticles	Anterior Outer lip Lira	Number of Axial Ribs Last Whorl	Number of Axial Ribs Pen. Whorl	Primary Spiral Cords Last Whorl	Length
<i>annae</i>	5	6–8	5–7	weak	10	10	9–10	12.9–15.6
<i>corinnae</i>	2–5 (5)	4–7 (6)	6–8 (6)	weak	6–13 (10)	7–10 (9)	9–12 (11)	9.2–14.8 (12.4)
<i>demani</i>	2–4 (3)	4–8 (6)	5–6 (5)	N	6–8 (7)	6–8 (7)	10–12 (12)	11.7–15.5 (13.8)
<i>goncalvesi</i>	1	3–5 (*)	6–7 (*)	N	obsolete	8–11 (10)	12–15 (12)	9.5–14.2 (11.5)
<i>karinae</i>	irregular	irregular	8–10 (*)	N	7–10 (9)	7–10 (9)	9–11 (9)	17.9–25.0 (20.1)
<i>lignaea</i>	5	5	5	Y	7	7	9–10	14.3
<i>permixta</i>	3–5 (4)	4–7 (5)	3–6 (5)	Y	7–10 (9)	8–10 (8)	7–10 (9)	9.4–16.1 (12.5)
<i>itzamnai</i>	2	5	4	N	8–10 (*)	8–10 (*)	11–13 (*)	17.4–17.8 (17.6)
<i>turbinella</i>	3–7 (4)	4–8 (6)	3–7 (6)	Y	8–13 (10)	9–14 (10)	6–10 (8)	6.6–14.9 (9.8)
<i>williamsae</i>	2–5 (4)	2–6 (*)	5–6 (5)	weak	8–10 (9)	9–10 (9)	9–11 (9)	11.5–15.0 (13.4)



**Figures 14–33.** *Engina corinnae* Crovo, 1974. **14–15.** Holotype, MCZ 277496, photo courtesy of Jennifer W. Lenihan, © Museum of Comparative Zoology, Harvard Univ., 13.0 mm. **16.** UF 128074, 27 m, off Boynton Beach, Palm Beach Co., Florida, 12.4 mm. **17.** EFG 9553, 38–43 m, off Boynton Beach, Palm Beach Co., Florida, 9.9 mm. **18.** UF 228793, 73 m, off Palm Beach, Palm Beach Co., Florida, 9.5 mm. **19.** UF 122778, 107 m, off Boynton Inlet, Palm Beach Co., Florida, 9.3 mm. **20.** UF 122778, 107 m, off Boynton Inlet, Palm Beach Co., Florida, 9.3 mm. **21.** UF 126241, 36.6 m, off Palm Beach, Palm Beach Co., Florida, 11.0 mm. **22.** MW, 30–46 m, off St. Augustine, St. Johns Co., Florida, 12.7 mm. **23.** HGL, 183–213 m, off Looe Key, Monroe Co., Florida, 11.5 mm. **24.** HGL, 30–46 m, off St. Augustine, St. Johns Co., Florida, 12.2 mm. **25.** MW, 6.4 km off Panama City, Bay Co., Florida, 13.2 mm. **26.** HGL, 30–46 m, off St. Augustine, St. Johns Co., Florida, 10.5 mm. **27.** EFG 13895, 30 m, off West Palm Beach, Palm Beach Co., Florida, 14.2 mm. **28.** EFG 27567, 39 m, 54 km SSW of Panama City, Bay Co., Florida, 14.7 mm. **29.** MW, 27 m, off Panama City, Bay Co., Florida, 10.5 mm. **30.** MW, 31 m, off NE Yucatan, Mexico, 14.8 mm. **31.** EFG 28347, 61 m, off Egmont Key, Hillsborough Co., Florida, 12.6 mm. **32.** MW, 34 m, off Mayport, St. Johns Co., Florida, 12.7 mm. **33.** ?*Engina corinnae*. UF 352841, 18 m, off Boynton Beach, Palm Beach Co., Florida, 12.4 mm.



**Figure 34.** Distribution of *Engina corinnae* Crovo, 1974 (◎) and *Engina demani* de Jong and Coomans, 1988 (●).

Panama City, Bay Co.; EFG 27567 (1), 39 m, 54 km SSW of Panama City, Bay Co., 29° 43.32' N, -85° 54.85' W. Louisiana: EFG 23426 (1), 57–65 m, Ewing Bank, 105 km off Louisiana coast, 28° 06.07' N, -91° 02.42' W. Mexico: MW (3), 31 m, off NE Yucatán.

Lee (2009) also lists Xalvis Island, St. Johns Co., Florida.

**Distribution:** Western Atlantic Ocean, offshore, eastern Florida from St. Johns County to the Florida Keys. Gulf of Mexico from Hillsborough County, Florida, west to Louisiana, and off Yucatán Peninsula. The *E. corinnae* recorded from the East Flower Garden banks by Odé (1983) may be this species but we have not seen the specimen. This species co-occurs with the equally rare *E. williamsae* at Egmont Key off Tampa Bay, western Florida.

**Habitat:** Empty shells have been found from 18–122 m on rubble bottom. Live specimens have been recorded from 30–73 m. Specimens are locally common and are occasionally found on *Spondylus*. Most specimens are taken as by-catch by shrimp and scallop trawlers. A single label reads “rock, sand reef,” the only report of a habitat. Specimens are frequently covered by calcareous algae.

**Variation in Specimens:** Specimens vary in degree of coloration, from nearly all white (holotype) to having prominent brown patches. The intervarical brown banding varies from diffuse patches to distinctly pigmented spiral cords, but is always present. Specimens also vary in the degree of elongation, ranging from compact to rather fusiform.

**Etymology:** Named for Corinne E. Edwards (1905–1989), an “ardent collector of marine life as well as an

educator in popular subjects on natural history” (Crovo, 1974: 30).

**Comparison with Other Species:** *Engina corinnae* superficially resembles *E. williamsae* new species. *Engina corinnae* has more prominent spiral sculpture over the entire shell, including the sub-sutural band, which is nearly smooth in *E. williamsae*. *Engina corinnae* is also less solid, has a shorter spire, and averages a slightly smaller size. The widespread *E. turbinella* differs in its (usually) much darker coloration with white spots as contrasted to the lighter coloration with dark spots seen in *E. corinnae*, as well as its dark aperture with white teeth. See Table 1 for a comparison with other species.

**Discussion:** *Engina corinnae* is an offshore species that varies greatly in the degree of elongation and coloration. The holotype is not typical of the specimens usually seen. It is small, compact, nearly uniformly white, and has fewer axial ribs than average specimens.

#### *Engina demani* de Jong and Coomans, 1988 (Figures 34–49)

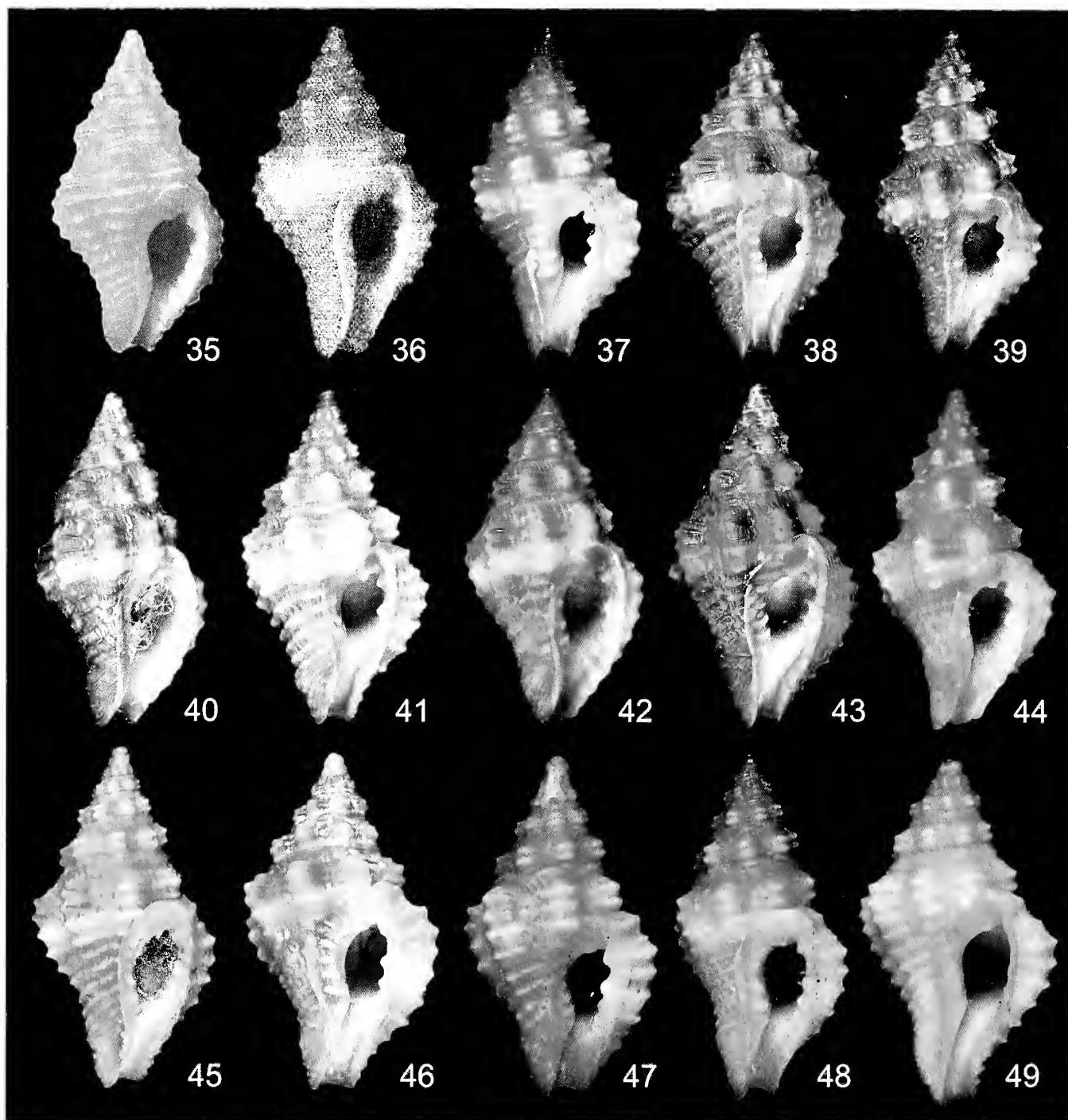
*Engina demani* de Jong and Coomans, 1988: 83, pl. 38, fig. 451; Faber, 2007: 74, figs. 1–3; Watters, 2009: 271.

*Engina janowskyi* Coltro, 2005: 1, pl. A, figs. 1–5; Faber, 2007: 74, figs. 6, 7; Dornellas and Simone, 2011: 20; Landau and Vermeij, 2012: 123, 125, 126.

*Hesperisternia janowskyi* (Coltro, 2005). — Watters, 2009: 271.

*Engina demanorum* [sic] de Jong and Coomans, 1988. — Landau and Vermeij, 2012: 123, 125, 126 [unjustified emendation, see “etymology” below].

**Description (based on 20 adult specimens):** Largest adult specimen, 15.5 mm in length; smallest specimen, 10.7 mm in length. Shell biconic to fusiform; spire ca. 50% total length. Protoconch small, conical, of 1.5–1.75 smooth, white or brown banded whorls. Teleoconch of 5.5 whorls, weakly demarcated from protoconch. Teleoconch sculpture of 10–12 (mode=12) evenly spaced, rounded, spiral cords between the suture and the anterior limit of the siphonal canal. Subsutural slope wide, flat, with single primary thread, well-developed in some specimens, very weak in others. Between these cords are ca. 10 fine, regular threads. Axial sculpture of widely spaced, wide, primary angular ribs; 7 (rarely 6 or 8) on the final whorl, 7 (rarely 6 or 8) on penultimate whorl, most prominent on periphery, with numerous secondary fine, axial threads in between primary ribs; in well-preserved specimens these threads are developed into oblique lamella, giving a scalloped appearance to the sculpture. Terminal varix well-developed, angular. Aperture oval. Parietal wall erect on anterior half. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 5 (rarely 6) small denticles. The thin rib that projects deep



**Figures 35–49.** *Engina demani* de Jong and Coomans, 1988. **35.** Holotype, *Engina demani* de Jong and Coomans, 1988, 11.0 mm, photo courtesy of Marien Faber. **36.** Holotype, *Engina janowskyi* Coltro, 2005, 13.2 mm, reproduced from Coltro (2005). **37.** HGL, 183 m, 3.2 km W of Sandy Lane Bay, Barbados, 11.2 mm. **38.** GTW 13795e, 4 m, Ilha Escalvada, Espírito Santo State, Brazil, 13.8 mm. **39.** GTW 13795e, 4 m, Ilha Escalvada, Espírito Santo State, Brazil, 15.2 mm. **40.** HGL, 40–45 m, off Búzios, São Paulo State, Brazil, 10.7 mm. **41.** HGL, shallow water, Cartagena, Colombia, 13.6 mm. **42.** GTW 13795a, 40–45 m, Ilha de Cabo Frio, Rio de Janeiro State, Brazil, 13.5 mm. **43.** GTW 12026d, 3 m, off Guarapari, Espírito Santo State, Brazil, 15.0 mm. **44.** GTW 15579a, French Guiana, 13.1 mm. **45.** GTW 13795b, 4 m, Ilha Escalvada, Espírito Santo State, Brazil, 15.3 mm. **46.** GTW 11645a, 15–25 m, off Guarapari, Espírito Santo State, Brazil, 12.3 mm. **47.** GTW 13795e, 4 m, Ilha Escalvada, Espírito Santo State, Brazil, 12.3 mm. **48.** GTW 13795b, 4 m, Ilha Escalvada, Espírito Santo State, Brazil, 11.4 mm. **49.** GTW 13795e, off Guarapari, Espírito Santo State, Brazil, 14.9 mm.

into the aperture and delimits the siphonal canal found in other species is absent or nearly so. Radial lirae 1–4 (mode=3) (may be bi- or trifurcate) at posterior end, weak and irregular, not very distinct from columellar folds. Anterior to these are columellar folds (4–8, mode=6) weak, irregular, often limited to edge of parietal wall. Swelling on interior ledge of columella not pronounced. Siphonal canal moderately short, open. Base color variable: dark brown, tan, or yellow, axial ribs usually darker, always with a continuous pale band just anterior to the periphery. The abapertural side of the axial ribs is usually dark-colored and the adapertural side is usually pale. Aperture white to tan, the siphonal canal rimmed in brown. Operculum oval, yellow-brown, with a subterminal nucleus. Radula and anatomy unknown.

**Holotype:** *Engina demani* de Jong and Coomans, 1988: ZMA 3.87.084; *Engina janowskyi* Coltro, 2005: Museu de Zoologia da Universidade de São Paulo 37178, but apparently lost (*fide* D. Cavallari, Jan. 2015).

**Type Locality:** *Engina demani* de Jong and Coomans, 1988, Aruba, harbour [Netherlands Antilles]. *Engina janowskyi* Coltro, 2005, off Guarapari, Espírito Santo State, Brazil.

**Paratype(s):** *Engina demani* de Jong and Coomans, 1988: Faber (2007) illustrated a “paratype” from the Frère Fredericus Verberne collection. Although de Jong and Coomans (1988) mentioned additional examples in the Verberne and de Man collections, they are not explicitly referred to as types and it is not certain whether these specimens are valid paratypes. *Engina janowskyi* Coltro, 2005: Museu Oceanográfico Eliézer Rios da Funfação Universidade de Rio Grande 43853; Museu Nacional da Universidade Federal do Rio de Janeiro, unnumbered; P.M. Santos Costa coll.; R. Janowsky coll. [all single specimens]. The localities of the paratypes were not given but are presumed to be from the type locality.

**Other Material Examined (28 specimens):** Barbados: HGL (1), 183 m, 3.2 km W of Sandy Lane Bay. Colombia: HGL (1), shallow water, Cartagena. French Guiana: GTW 15579a (1). Brazil: GTW 11645a (3), HGL (1), 15–25 m, off Guarapari, Espírito Santo State; GTW 13795c (1), 25 m, off Guarapari, Espírito Santo State; GTW 12026c (2), 12026d (4), 3 m, off Guarapari, Espírito Santo State; HGL (1), 18 m, off Anchieta, Espírito Santo State; GTW 13795b (3), 13795e (5), 4 m, Ilha Escalvada, Espírito Santo State; GTW 13795a (1), 40–45 m, Ilha de Cabo Frio, Rio de Janeiro State; HGL (1), 34–45 m, off Búzios, São Paulo State; HGL (3), 40–45 m, off Búzios, São Paulo State.

**Distribution:** Apparently widely distributed across the southern Caribbean and down the Brazilian coast to São Paulo State, but this is based on few records with large gaps.

**Habitat:** Empty shells are found at depths between 3–183 m; some live specimens have been collected in caves at 40–45 m, but the majority of specimens examined were found on rubble or under rocks from 4 m.

**Variation in Specimens:** Shell base color varies from nearly pure white to nearly all dark brown. Elongation varies from compact, solid shells (typically from Brazil, Figures 38, 43) to relatively high-spired, narrow shells (French Guiana, Figure 44). Despite this great variation in color and elongation of the shell, the sculpture is remarkably uniform in the number of axial and spiral elements.

**Etymology:** *Engina demani* de Jong and Coomans, 1988, named for Ad and Gon de Man, shell collectors in Aruba. Thus the correct orthography should be *demanorum*. However, a name change reflecting this would be an unjustified emendation. *Engina janowskyi* Coltro, 2005, named for Robert H. Janowsky, owner of MdM Shell Books in Wellington, Florida, USA.

**Comparison with Other Species:** Some color forms of *E. permixta* are similar to *E. demani*, with which it may be sympatric. *Engina permixta* has more axial ribs on both the final whorl (7–10) and the penultimate whorl (8–10) than does *E. demani* (6–8 for both) and has fewer spiral cords on the final whorl (7–10 vs. 10–12). Additionally, the deep ridge bounding the siphonal canal on the inside of the outer lip is present in *E. permixta* but absent or very weak in *E. demani*. See Table 1 for a comparison with other species.

**Discussion:** This is a very variable species in coloration, in degree of elongation, and in the strength of the sculpture. *Engina demani* is based on short, compact specimens. *Engina janowskyi* is based on elongate forms. Without seeing intermediates, the two forms would clearly seem to represent two taxa. However, there is no clear cut delineation between the two forms in either color or elongation and the two taxa are synonymous. This possible synonymy was first suggested by Faber (2007), who remarked that *E. demani* may be the shallow water form and *E. janowskyi* the deeper water form. However, our records indicate that there is great variation within each population regardless of depth and both “forms” and intergrades co-occur together.

#### *Engina goncalvesi* Coltro, 2005 (Figures 5–9, 13)

*Engina goncalvesi* Coltro, 2005: 1–2, pl. B, figs. 1–11; Faber, 2007: 74 [in synonymy of *Bailya milleri* Nowell-Usticke, 1959]; Watters, 2009: 270–271, figs. 190, 191; Dornellas and Simone, 2011: 17; Landau and Vermeij, 2012: 123.

**Description (based on 4 adult specimens):** Largest adult specimen, 14.2 mm in length; smallest specimen, 9.5 mm in length. Shell fusiform; spire ca. 50% total length. Protoconch small, of 1.5 smooth, brown whorls

with pale peripheral band. Teleoconch of 5 whorls, abruptly arising from protoconch. Teleoconch sculpture of 12–15 (mode=12) primary flattened, spiral threads on final whorl between the suture and the anterior limit of the siphonal canal, with numerous intercalated secondary and tertiary threads. Spiral cords on siphonal canal slightly stronger. Axial sculpture of broad, low ribs; ca. 20 primary ribs on penultimate whorl, obsolete on most specimens by last whorl. Intersections of axial and spiral sculpture with weak, elongated nodules. Terminal varix well-developed, flaring, moderately narrow. Aperture oval. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 6–7 weak, irregular denticles. The thin rib that projects deep into the aperture and delimits the siphonal canal found in other species is absent. Single (or bifurcating) radial lira at posterior end, very weak and irregular, not very distinct from columellar folds. Anterior to this lira are columellar folds (3–5), usually indistinct, irregular, often limited to edge of parietal wall. Swelling on interior ledge of columella distinct, white. Parietal lip erect for most of its length. Siphonal canal short, open. Color brown with wide, pale tan spiral band at subperiphery, primary spiral cords often darker. Aperture with brownish-purple tinge. Operculum leaf-shaped, golden-tan, with anterior terminal nucleus. Radula and anatomy unknown.

**Holotype:** Stated to be in Museu de Zoologia da Universidade de São Paulo, 37179, and listed as such in Dornellas and Simone (2011), but not found (*fide* L. R. L. Simone, pers. comm., 2008).

**Type Locality:** Off Cabo Frio, Rio de Janeiro State, Brazil. Depth unknown.

**Paratype(s):** Museu Oceanográfico Eliézer Rios da Fundação Universidade de Rio Grande 43854 (1); Museu Nacional da Universidade Federal do Rio de Janeiro, unnumbered (2); P.M. Santos Costa coll. (1). The localities of the paratypes were not given but are presumed to be from the type locality.

**Other Material Examined (4 specimens): Brazil.** GTW 10479a (1), 12477a (1), 40–50 m, in cave, off Arraial do Cabo, Rio de Janeiro State; HGL (1), 40–44 m, in cave, off Arraial do Cabo, Rio de Janeiro State; GTW 12477b (1), 150–160 m, off Cabo Frio, Rio de Janeiro State.

**Distribution:** Brazil, between Cabo Frio, Rio de Janeiro State, and Ilhabela, São Paulo State.

**Habitat:** Empty shells are found between depths of 25–160 m; live individuals from 25–45 m under rocks, sometimes in caves.

**Variation in Specimens:** The few specimens we have seen are very uniform in all characteristics.

**Etymology:** Named for Paulo Cesar Pinto Gonçalves, who first collected the species.

**Comparison with Other Species:** The near lack of axial sculpture on the final whorl and reduced columellar dentition set this species apart from all other western Atlantic *Engina*. See Table 1 for a comparison with other species.

**Discussion:** This species is placed in *Engina* with some reservation. The parietal shield lirae and columellar folds are nearly absent in some specimens and only barely expressed in the remainder.

***Engina itzamnai* (Watters, 2009)**  
**(Figures 50–57, 68)**

*Hesperisternia itzamnai* Watters, 2009: 271, figs. 192–195, 264.

*Engina itzamnai* (Watters, 2009). — Landau and Vermeij, 2012: 123.

*Engina dicksoni* Petuch, 2013: 72, 192, 202, fig. 5.6E.

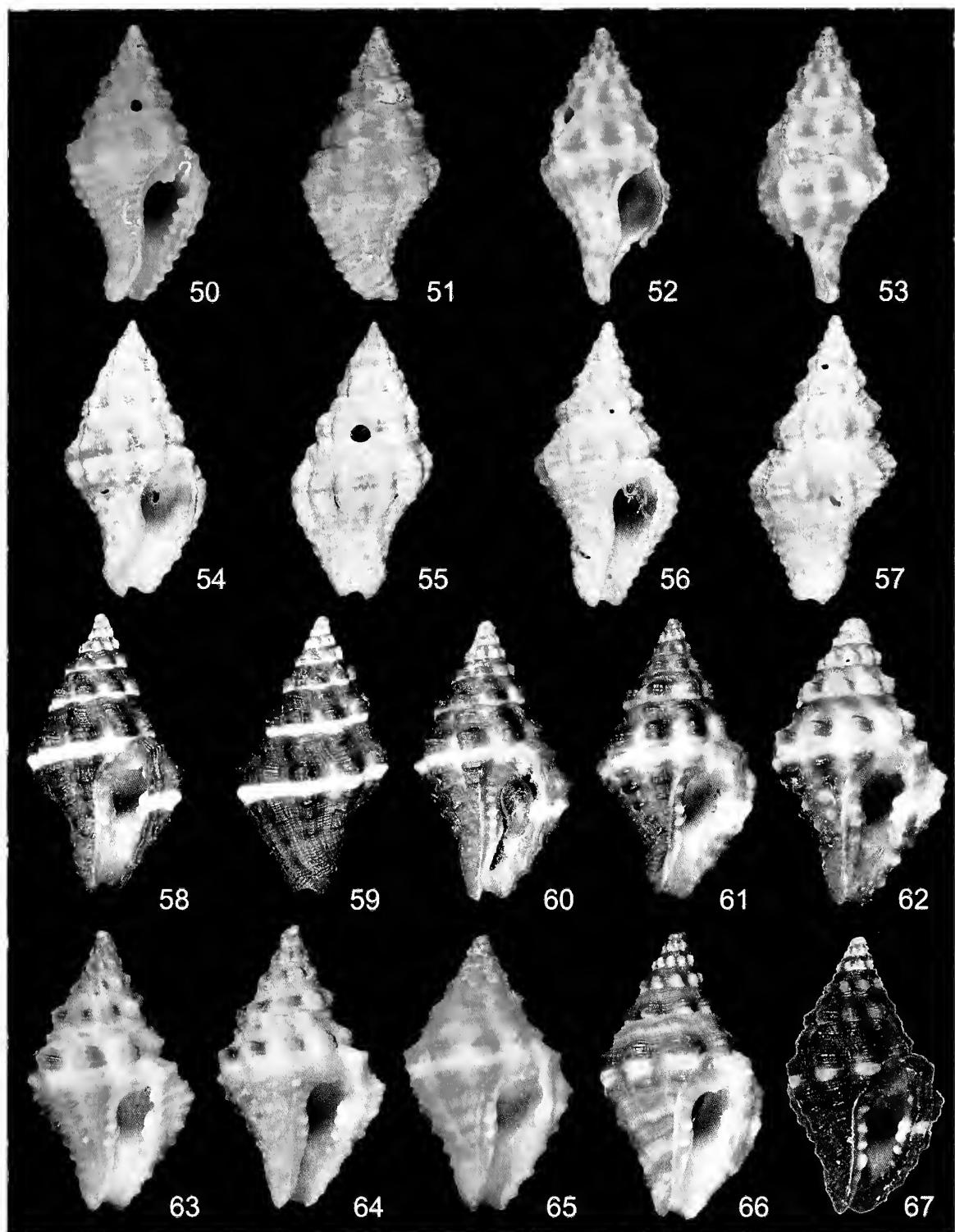
**Description (based on 4 specimens):** Largest adult specimen, 17.8 mm in length (holotype); smallest adult specimen, 17.4 mm in length. Shell fusiform; spire ca. 50% total length. Shell relatively thin. Protoconch small, conical, of 1.5 smooth, white whorls with tan blotches. Teleoconch of 5.5 whorls, strongly demarcated from protoconch. Teleoconch sculpture of 11–13 rounded, widely separated primary spiral cords between the suture and the anterior limit of the siphonal canal, with numerous intercalated secondary threads. Subsutural slope wide, flat, with single primary thread. Spiral cords on siphonal canal slightly stronger. Axial sculpture of widely spaced, rounded primary ribs; 8–10 on penultimate whorl, 8–10 on final whorl, with numerous secondary axial threads. Intersections of axial and spiral sculpture with strong, elongated nodules, strongest at periphery. Terminal varix weakly developed, somewhat constricted, narrow. Aperture oval, outer lip with 4 medial teeth. Anal canal deeply indented between two teeth; columellar tooth bifid. Parietal wall erect with 7 weak, lirate teeth. Siphonal canal moderately long, open. Color white with orangish-tan interaxial spaces cut by a white subperipheral narrow band; the spaces form broken flammulations below this band. Aperture white. Operculum, radula, and anatomy unknown.

**Holotype:** *Hesperisternia itzamnai* Watters, 2009, UF 170226. *Engina dicksoni* Petuch, 2013, UF 328420.

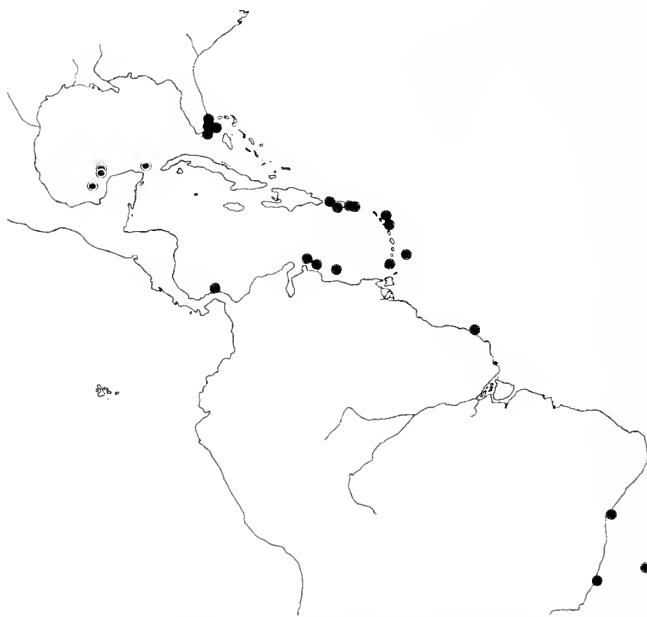
**Type Locality:** *Hesperisternia itzamnai* Watters, 2009: 100 fms. [91 m], NE of Contoy Light, Isla Contoy, Quintana Roo State, México: *Engina dicksoni* Petuch, 2013: 35 m depth on Campeche Bank, off Puerto Progreso, Yucatán State, Mexico.

**Paratype(s):** *Hesperisternia itzamnai* Watters, 2009, UF 425817 (1), from type locality. *Engina dicksoni* Petuch, 2013, Petuch coll. (1), from type locality.

**Other Material Examined (2 specimens):** Mexico: EFG 25800 (1), 52–53 m, 64 km NW of Cayos



**Figures 50–67.** *Engina* species. **50–57.** *Engina itzamnai* (Watters, 2009). **50–51.** Holotype, UF 170226, 17.9 mm. **52–53.** Paratype, UF 425817, 91 m, NE of Contoy Light, Isla Contoy, Quintana Roo State, Mexico, 16.2 mm. **54–55.** MW, 31 m, off NE Yucatan, Campeche State, Mexico, 17.4 mm. **56–57.** EFG 25800, 52–53 m, 64 km NNW of Cayos Arcas, Campeche Bank, Campeche State, Mexico, 17.4 mm. **58–67.** *Engina permixta* new species. **58–59.** Holotype, UF 479326, 16.1 mm. **60.** Paratype, UF 479324, from type locality, 14.5 mm. **61.** Paratype, OSUM 39958, 21 m, off Piúma, Espírito Santo State, Brazil, 12.7 mm. **62.** GTW 4265f, 20–25 m, off Guarapari, Espírito Santo State, Brazil, 11.4 mm. **63.** GTW 4265b, 21 m, off Piúma, Espírito Santo State, Brazil, 13.0 mm. **64.** GTW 13807a, 40–50 m, off Conceição da Barra, Espírito Santo State, Brazil, 12.0 mm. **65.** GTW 4265r, from type locality, 12.1 mm. **66.** GTW 12026a, 40–45 m, off Búzios, Rio de Janeiro State, Brazil, 11.2 mm. **67.** GTW 4265ah, 10–15 m, Porto da Barra, Salvador, Bahia State, Brazil, 12.4 mm.



**Figure 68.** Distribution of *Engina itzamnai* (Watters, 2009) (◎) and *Hesperisternia karinae* (Nowell-Usticke, 1959) (●).

Areas, Campeche Bank, Campeche State,  $20^{\circ} 45.59' N$ ,  $-92^{\circ} 12.63' W$ ; MW (1), 31 m, off NE Yucatán, Campeche State.

**Distribution:** Gulf of Mexico, Campeche Bank between Arrecife Alacrán and Cayos Areas.

**Habitat:** Dead specimens were dredged in 46–180 m on rubble bottom. No live collected specimens are known to us.

**Variation in Specimens:** The few known specimens vary slightly in the number of axial (8–10) and spiral (11–13) sculptural elements.

**Etymology:** *Hesperisternia itzamnai* Watters, 2009: Mayan, *Itzamná*, the creator deity in Mayan mythology. This species is only known from off the Yucatán Peninsula, ancestral home of the Mayans. A masculine name. *Engina dicksoni* Petueh, 2013: Named for Andrew Dickson, collector of the type.

**Comparison with Other Species:** This is the largest western Atlantic *Engina* and the most fusiform. See comparison with *E. lignea* new species, below. See Table 1 for a comparison with other species.

**Discussion:** This is apparently a very rare species in collections. Petuch (2013) renamed this taxon *Engina dicksoni*.

#### *Engina lignea* new species (Figures 10–13)

**Description (based on 2 specimens):** Only adult specimen seen, holotype 14.3 mm in length  $\times$  7.4 mm in width. Fusiform; spire ca. 50% total length. Shell thick,

solid. Protoconch small, conical, of 1.5 smooth, tan whorls. Teleoconch of 5 whorls, strongly demarcated from protoconch. Teleoconch sculpture of 9–10 rounded, widely separated primary spiral cords between the suture and the anterior limit of the siphonal canal, with 3–6 intercalated secondary threads. Subsutural slope wide, flat, with single primary thread. Axial sculpture of widely spaced, rounded primary ribs; 7 on penultimate whorl, 7 on final whorl, with numerous secondary very fine, axial threads. Intersections of axial and spiral sculpture with strong, elongated nodules, strongest at periphery. Terminal varix weakly developed, low and wide. Aperture oval, outer lip with 5 lirate denticles extending steep into aperture. Anal canal shallowly indented between two weak teeth. Parietal wall erect anteriorly with 5 lirate columellar folds. Siphonal canal moderately long, open. Color uniformly light tan to brown, with a vague darker band on sub-sutural plane, with or without lighter-colored peripheral axial nodes. Aperture light tan. Operculum, radula, and anatomy unknown.

**Holotype:** UF 479325 (ex EFG 26687).

**Type Locality:** 46–48 m, 145 km WSW of Arrecife Alacrán, Campeche Bank, Campeche State, México,  $22^{\circ} 10.80' N$ ,  $-91^{\circ} 09.00' W$ .

**Paratype(s):** BMSM 76001(1), 50–55 m, 146 km WSW of Arrecife Alacrán, Campeche Bank, Campeche State, México,  $22^{\circ} 11.46' N$ ,  $-91^{\circ} 08.71' W$  (ex EFG 25822).

**Distribution:** Known only from off northern Yucatán Peninsula.

**Habitat:** Only empty shells have been found between 46–55 m.

**Variation in Specimens:** The two known specimens differ in color from light tan to dark brown.

**Etymology:** Latin *ligneus*, made of wood, in reference to the texture and colors of the shells.

**Comparison with Other Species:** This species is most similar to the sympatric *E. itzamnai*. It is a smaller species that differs in having fewer primary axial ribs on both the final whorl (8–10 in *E. itzamnai*, 7 in *E. lignea*) and on the penultimate whorl (8–10 in *E. itzamnai*, 7 in *E. lignea*), as well as fewer primary spiral cords (11–13 in *E. itzamnai*, 9–10 in *E. lignea*). See Table 1 for a comparison with other species.

**Discussion:** This is the second new *Engina* described from the Yucatán Peninsula. Both are deeper water species that are rare in collections. Both have some characteristics of *Hesperisternia* but based on the analysis of Landau and Vermeij (2012) we have placed them in *Engina*.

#### *Engina permixta* new species (Figures 58–67, 103)

non *Engina turbinella* (Kiener, 1836). — Rios, 1975: 93, pl. 27, fig. 385; Coltro, 2005: 1, pl. A, figs. 8–10 [misidentifications].

?*Engina turbinella* (Kiener, 1836). — Lopes and Alvarenga, 1955: 173; Kempf and Matthews, 1968: 93; Matthews and Kempf, 1970: 32, 46; Eston et al., 1986: 43; Leal, 1991: 153.

**Description (based on 31 adult specimens):** Largest adult specimen, 16.1 mm in length (holotype); smallest specimen, 9.4 mm in length; holotype 16.1 in length  $\times$  8.3 mm in width. Shell biconic; spire ca. 50% total length. Protoconch small, conical, of 1.5 smooth, white or brown banded whorls; last  $\frac{1}{4}$  whorl may have axial folds. Teleoconch of 5.5 whorls, strongly demarcated from protoconch. Teleoconch sculpture of 7–10 (mode=9) primary spiral cords between the suture and the anterior limit of the siphonal canal. Subsutural slope wide, flat, with single primary cord. Three primary cords gathered at periphery, remaining cords very widely spaced, flattened or nodulose. 5–6 uniformly wide secondary threads between these remaining cords. Axial sculpture of widely spaced, angular primary ribs; 7–10 (mode=9, but often 8) on the final whorl, 8–10 (mode=8) on penultimate whorl, axial sculpture most prominent on periphery, with numerous secondary fine, axial threads in between primary ribs. Terminal varix only slightly more prominent than preceding axial ribs, angular. Aperture oval. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 3–6 (mode=5) weak, irregular denticles, posterior-most 2 often fused. The thin rib that projects deep into the aperture and delimits the siphonal canal found in other species is weak but always present. 3–5 (mode=4) radial lira present at posterior end, weak and irregular, not very distinct from columellar folds. Anterior to these are 3–7 (mode=5) denticulate columellar folds, irregular, often limited to edge of parietal wall. Second or third anterior denticle often extending deep into aperture. Anterior-most denticle may form a ridge extending along the parietal wall to the anterior margin. Interior ledge of columella well-defined, often merging with anterior-most denticle. Siphonal canal moderately short, open. Base color variable: dark brown, tan, or yellow, axial ribs usually darker, always with a continuous white band just anterior to the periphery; this band may have yellow portions to it. Aperture white to tan. Operculum oval, yellow-brown, with a subterminal nucleus. Radula and anatomy unknown.

**Holotype:** UF 479326 (ex GTW 4265r).

**Type Locality:** 1 m, Cajueiro, Rio Grande do Norte State, Brazil.

**Paratype(s):** BMSM 76000 (1), from type locality (ex GTW 4265r); OSUM 39958 (1), 21 m, off Piúma, Espírito Santo State, Brazil (ex GTW 13807b); UF 479324 (1), from type locality (ex GTW 4265r). Other Material Exam-

ined (51 specimens): Brazil: GTW 13807c (6), 1 m, Cajueiro, Rio Grande do Norte State; MW (3), intertidal, Ilha do Frade, Fernando de Noronha, Pernambuco State; UF 126233 (2), Ponta Verde, Maceió, Alagoas State; MW (1), 1 m, Maragogi, Alagoas State; GTW 4265ah (2), EFG 14667 (3), 10–15 m, Porto da Barra, Salvador, Bahia State; MW (5), Monte Serrat, Bahia State; MW (1), Barra, Salvador, Bahia State; GTW 13807a (1), 40–50 m, off Conceição da Barra, Espírito Santo State; GTW 13807b (2), KF 7343 (1), 21 m, off Piúma, Espírito Santo State; HGL (1), 15–25 m, off Guarapari, Espírito Santo State; GTW 4265f (1), GTW 4265o (1), GTW 4265s (2), HGL (2), 20–25 m, off Guarapari, Espírito Santo State; HGL (1), 10–25 m, off Guarapari, Espírito Santo State; GTW 13807d (2), 60–80 m, off Guarapari, Espírito Santo State; KF 6123, 45–60 m, off Guarapari, Espírito Santo State (1); KF 4928, 15–30 m, off Guarapari, Espírito Santo State (2); KF 80 (1), Rio de Janeiro, Rio de Janeiro State; GTW 12026a (6), GTW 12026b (1), HGL (1), 40–45 m, off Búzios, Rio de Janeiro State; HGL (1), 35–45 m, off Búzios, Rio de Janeiro State; HGL (1), 40–46 m, off Búzios, Rio de Janeiro State.

**Distribution:** Brazil, from Rio Grande do Norte State to São Paulo State; Fernando de Noronha. If the specimens referred to *E. turbinella* by Leal (1991) are this species, then it is also present at Abrolhos, Atol das Rocas, Jaseur, and Davis and Dogaressa seamounts.

**Habitat:** Empty shells have been found from low tide to 50 m; live individuals have been found from 1–45 m under rocks and on rubble.

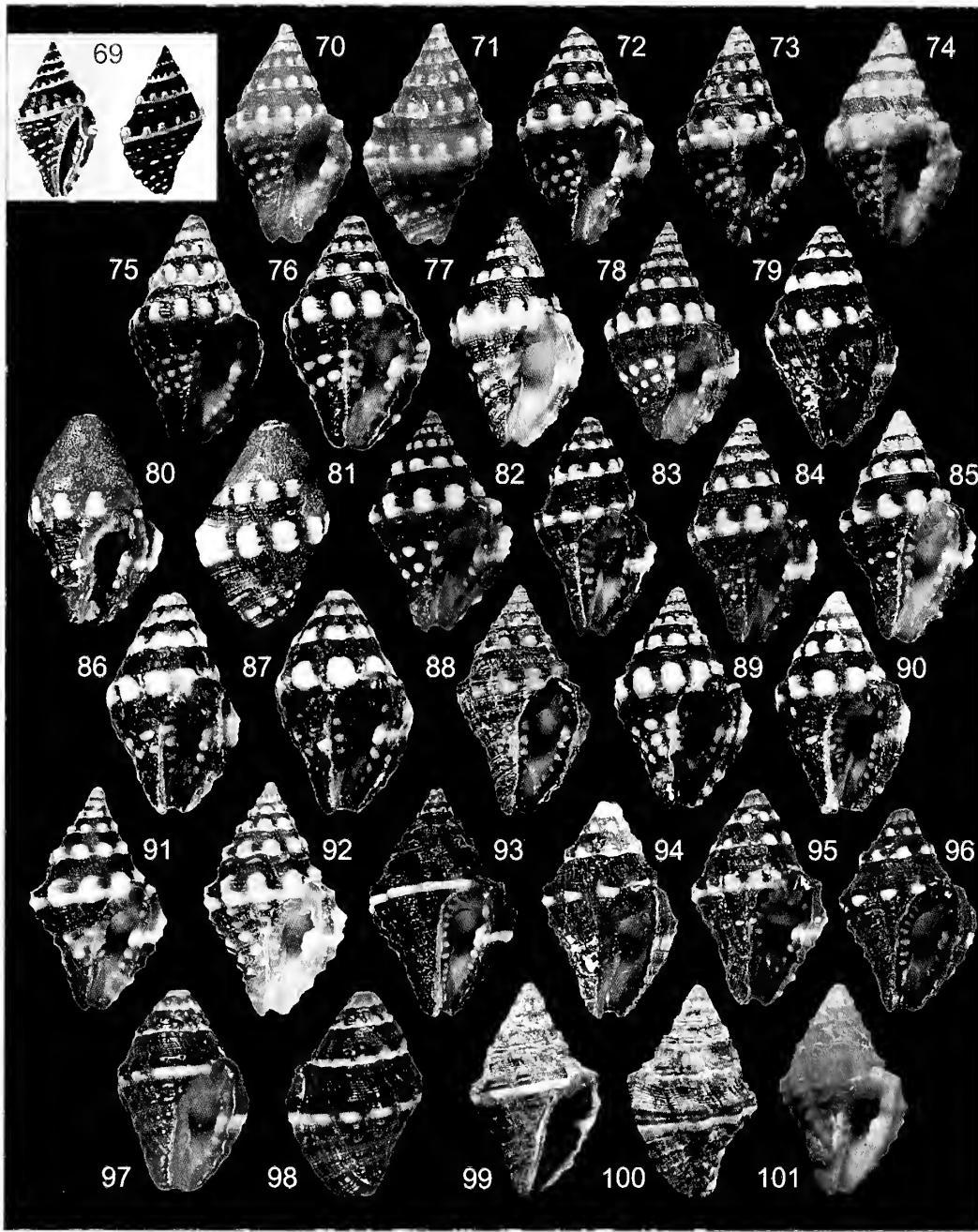
**Variation in Specimens:** Shell coloration varies from nearly all dark brown to nearly all pale yellow to white, with all intergrades. There is no clinal variation in shell color and all colors may occur together. The dark brown morph characterized by the holotype appears to be the most common.

**Etymology:** Latin *permixta*, mixed, confused, in relation to the disarray of color forms.

**Comparison with Other Species:** Although often misidentified as *E. corinnae*, it is not similar to that Florida-Gulf of Mexico species. It is most similar to some color forms of *E. demani*, with which it may co-occur. See the comparison under that species for details. See Table 1 for a comparison with other species.

**Discussion:** The somewhat weathered lectotype of *Engina zonata* Gray, 1839, is very close to some specimens of this species. However, the paralectotype clearly shows the presence of sub-peripheral white nodules, which do not occur in *E. permixta*.

***Engina turbinella* (Kiener, 1836)**  
(Figures 69–100, 102)



**Figures 69–101.** *Engina* species. **69–100.** *Engina turbinella* (Kiener, 1836). **69.** *Purpura turbinella* Kiener, 1836: 29, pl. 9, fig. 25. **70–71.** UF 281377, Scarborough, Tobago. 12.1 mm. **72.** KF 4735, Punto San Juan, Venezuela. 12.3 mm. **73.** UF 281378, Friendship Beach, Tobago. 11.1 mm. **74.** EFG, 60 ft., Montexuma Shoals, Mustique Island. 12.7 mm. **75.** HGL, drift, Playa de Carenera, Venezuela. 9.6 mm. **76.** EFG 25590, 3 km N of Colón Island, Panamá. 8.8 mm. **77.** GTW 4265af, 1–2 m, Buraco da Rachel, Fernando de Noronha, 9.3 mm. **78.** UF 70393, Bruja Point, Canal Zone, 15.0 mm. **79.** GTW 4265e, 0.3–1.5 m, Punta Robles, Ambergris Caye, Belize, 13.2 mm. **80–81.** NHMUK 1982122, syntype of *Engina elegans* Gray, 1839, ca. 7.5 mm, photo courtesy of Phil Hurst, NHMUK. **82.** HGL, Isla de Utila, Honduras, 11.3 mm. **83.** GTW 4265ag, 2–5 m, Isla la Tortuga, Venezuela, 13.3. **84.** GTW 4265b, 7.3 m, Isla Morro Pelotas, Venezuela, 14.2 mm. **85.** UF 146654, Miami, Miami-Dade Co., Florida, 14.0 mm. **86.** GTW 4265h, 0.3–1.5 m, Long Reef, Isla Roatán, Honduras, 8.6 mm. **87.** GTW 4265c, 1 m, Sandbar Reef, Ambergris Caye, Belize, 9.3 mm. **88.** EFG 19507, Isla de Providencia, Colombia, 13.9 mm. **89.** EFG 25673, Bocas del Toro, Panamá, 10.4 mm. **90.** MW, 1.0–1.5 m, Sand Key, off Key West, Monroe Co., Florida, 11.0 mm. **91.** KF 2503, 12 m, St. Vincent, S end of Baliceaux Island, Grenadines, 12.3 mm. **92.** MW, Pompano Beach, Broward Co., Florida, 13.5 mm. **93.** KF 2551, 8–9 m, Cannoun Island, Grenadines, 13.7 mm. **94.** HGL, Current, Eleuthera, 12.1 mm. **95.** GTW 4265w, 0.6–1.8 m, Coral Cove, Mt. Hartman Bay, Grenada, 10.5 mm. **96.** GTW 4265aa, 0.3–1 m, Enrique, La Parguera, Puerto Rico, 9.7 mm. **97–98.** UF 126216, paratype of *Engina turbinella cruzana* (Nowell-Usticke, 1959), 9.2 mm. **99–100.** NHMUK 1982122, lectotype of *Engina zonata* Gray, 1839, 11.5 mm. **101.** *Engina* cf. *turbinella*. KF 5262, 12 m, Savan Island, Grenadines, 12.2 mm.



**Figure 102.** Distribution of *Engina permixta* new species (○) and *Engina turbinella* (Kiener, 1836) (●) (not shown, *E. turbinella* record from Fernando de Noronha).

*Buccinum B.r. parvum, striatum, asperum, ex albo...*  
Lister, 1685: pl. 953, fig. 3.

*Purpura turbinella* Kiener, 1836: 29, pl. 9, fig. 25.

*Engina zonata* Gray, 1839: 113; Tryon, 1883: 196, 247; Bartsch, 1931: pl. 1, fig. 6; Faber, 2007: 73 [in synonymy of *Purpura turbinella* Kiener, 1836]; Fraussen and Chino, 2011: 64 [in synonymy of *Purpura turbinella* Kiener, 1836]; Landau and Vermeij, 2012: 122 [in synonymy of *Purpura turbinella* Kiener, 1836].

*Engina elegans* Gray, 1839: 113; Tryon, 1883: 192; 213 [in synonymy of *Purpura turbinella* Kiener, 1836]; Pace, 1902: 78.

*Ricinula turbinella* (Kiener, 1836). — Reeve, 1846: species 42, pl. 5, fig. 42.

*Enzina* [sic] *zonata* Gray, 1847: 133; Tomlin, 1928: 40.

*Turbinella (Fusus) elegans* (Gray, 1839). — Tryon, 1881: 97.

*Engina turbinella* (Kiener, 1836). — Tryon, 1883: 192, 213, 244, pl. 62, figs. 38, 39; Dall and Simpson, 1901: 402; Warmke and Abbott, 1961: 116, pl. 21, fig. d; Orr, 1962: text fig. [radula], pl. 10, fig. B; Woodring, 1973: 477–478, pl. 74, figs. 4, 5; Abbott, 1974: 218, fig. 2399; Odé, 1983: 60, fig. 7; de Jong and Coomans, 1988: 82–83, pl. 38, fig. 450; Merlano and Hedegus, 1994: 187, fig. 710; Redfern, 2001: 93, pl. 43, fig. 395; Coltro, 2005: 1, pl. A, figs. 6, 7; Faber, 2007: 74, figs. 4, 5; Massemin *et al.*, 2009: 148 and text figures; Tunnell *et al.*, 2010: 214; Fraussen and Chino, 2011: 64; Daccarett and Bossio, 2011: 95, fig. 448; Zhang, 2011: 119, figs. 404(1–3); Landau and Vermeij, 2012: 122–127; Redfern, 2013: 144, figs. 414a,b.

*Engina turbinella cruzana* Nowell-Usticke, 1959: vi, 68–69; Warmke and Abbott, 1961: 116 [as a form].

*Engina turbinella* var. *cruzana* Nowell-Usticke, 1959: 68–69; Nowell-Usticke, 1969: 17, pl. 2, fig. "789" [790]; Boyko and Cordeiro, 2001: 61.

**Description (based on 26 adult specimens):** Largest adult specimen, 14.9 mm in length; smallest specimen, 6.6 mm in length. Spire occupies 30–50% of total length. Protoconch minute, of 1.5 smooth whorls, tan with or without a darker band. Protoconch almost always eroded away, very rarely remaining in adult specimens. Teleoconch of 5–6 whorls. Spiral sculpture consists of 6–10 (mode=8) primary spiral cords; the wide subsutural slope has secondary threads and usually a single primary (rarely two, rarely absent) cord somewhere between the suture and the mid-point of the subsutural slope; this cord may abruptly turn posteriorly at the edge of the varix. The periphery has 2–3 primary cords grouped over the axial nodes and microscopic threads; anteriorly there are 3–7 wide, rounded ribs widely separated by 3–5 secondary threads. Axial sculpture 8–13 (mode=10) elongated, undulating peripheral nodes on the final whorl, 9–14 (mode=10) on the penultimate whorl; usually prominent but less so on small specimens. Terminal varix slightly more developed than previous axial sculpture. Aperture small, constricted. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 3–7 (mode=5) denticles; the denticles are elongate but not lirate and do not project far into the aperture. The posterior-most two denticles are usually the most prominent and are fused; the anterior-most denticle forming a strong, long, thin rib that projects deep into the aperture and delimits the siphonal canal. Radial lirae (3–7, mode=4) at posterior end, usually long and thin but often not well-differentiated from columellar folds. Anterior to these are columellar folds (4–8, mode=6), irregular, some pustulose, some lirate, often limited to edge of parietal wall, anterior-most best-developed and forming a ridge on the interior of the columella. In some specimens, particularly small ones, the posterior half of the columella may be deeply excavated. Background color usually dark brown to black, rarely orange in some southeastern populations. Axial ribs at periphery always colored white, either as distinct spots or merged into a single spiral band; these white spots may be limited to the adapertural side of the ribs. Elsewhere, intersections of axial and spiral sculpture may or may not be present as white spots. 1° spiral cord on sub-sutural band may be white at termination. Aperture dark brown to black, fading to a lighter shade interiorly; outer lip denticles white, columellar ridge white. Operculum rounded, leaf-shaped, yellow with brown central radius. Radula figured by Orr (1962). Anatomy unknown.

**Types:** *Purpura turbinella* Kiener, 1836: Types not located at the Muséum d'histoire naturelle de la Ville de Genève (Y. Finet, pers. comm., 2011), the Muséum national d'Histoire naturelle, Paris (online database, 2011), nor the Natural History Museum UK (K. Way,

pers. comm., 2011), and are presumed lost. *Engina elegans* Gray, 1839: Syntypes, NHMUK 1982122 (5). The specimens are heavily worn and/or immature. *Engina zonata* Gray, 1839: Lectotype and paralectotype, NHMUK 1967592; the lectotype is the larger of the two, designated by Orr (1962). *Engina turbinella cruzana* Nowell-Usticke, 1959: Lectotype, AMNH 198494, designated by Boyko and Cordeiro (2001) [although listed as a variety on page 68 of Nowell-Usticke, 1959, the name was immediately used as a subspecies on the same page as well as earlier on page vi], additional specimens implied but their disposition is unknown except for UF 126216, Judith's Fancy, St. Croix, 7 paralectotypes.

**Type Locality:** *Purpura turbinella* Kiener, 1836: "Unknown." *Engina elegans* Gray, 1839, Atlantic Ocean. *Engina zonata* Gray, 1839: Atlantic Ocean. Lectotype label reads "West Indies." *Engina turbinella cruzana* Nowell-Usticke, 1959: West Coast [place name]. Judith's Fancy. Christiansted Harbor [all St. Croix]. Restricted by Boyko and Cordeiro (2001) to West Coast but paralectotypes at UF are from Judith's Fancy.

**Other Material Examined (951 specimens):** Florida: UF 12718 (1), S of Lake Worth Inlet, Palm Beach Co.; UF 126238 (1), Boynton Beach, Palm Beach Co.; MW (3), 18 m, Boynton Beach, Palm Beach Co.; UF 394034 (2), Hillsborough Light, Broward Co.; MW (2), 18 m, Pompano Beach, Broward Co.; UF 146654 (1), Miami, Miami-Dade Co.; UF 185179 (1), Bear Cut, Key Biscayne, Miami, Miami-Dade Co.; UF 126219 (4), Miami County Causeway, Miami-Dade Co.; UF 126227 (11), Biscayne Bay, Miami, Miami-Dade Co.; UF 238288 (3), Miami Beach, Miami-Dade Co.; UF 80978 (1), Key Largo, Monroe Co.; UF 239825 (1), Marathon, Key Largo, Monroe Co.; HGL (9), 3–4.5 m, Pickles Reef, Key Largo, Monroe Co.; UF 126223 (11), Little Molasses Reef, Key Largo, Monroe Co.; UF 80975 (2), Molasses Reef, Key Largo, Monroe Co.; UF 126228 (1), 4.0 km WSW of Carysfort Reef Light, Key Largo, Monroe Co.; UF 37855 (1), Dry Rocks, Key Largo, Monroe Co.; UF 123130 (51), UF 352066 (7), Looe Key, Big Pine Key, Monroe Co.; UF 352068 (6), UF 123056 (2), Little Torch Key, Monroe Co.; UF 61023 (4), UF 70396 (11), UF 192067 (3), Key West, Monroe Co.; UF 126218 (44), UF 126243 (92), UF 153382 (9), Middle Sambo Shoals, Key West, Monroe Co.; UF 80974 (41), Sambo Shoals, Key West, Monroe Co.; UF 126236 (3), Sand Key Light, Key West, Monroe Co.; UF 12714 (2), UF 70395 (3), UF 126231 (20), UF 192158 (2), MW (1), Pelican Shoals, Key West, Monroe Co.; UF 126222 (3), Washerwoman's Shoals, Key West, Monroe Co.; MW (7), 1.0–1.5 m, Sand Key, off Key West, Monroe Co.; UF 12717 (1), UF 126239 (13), Ft. Jefferson, Dry Tortugas, Monroe Co.; UF 12715 (1), Bush Key Reef, Dry Tortugas, Monroe Co.; UF 12716 (1), Garden Key, Dry Tortugas, Monroe Co. Bahamas: UF 126240 (5), North Bimini; GTW 4265a (1), tide pool, South Bimini; UF 126246 (10), Gun Cay, off Bimini; UF 80985 (1), Grand Bahama Island; UF

37853 (2), West End, Grand Bahama Island; UF 70391 (2), New Providence; UF 126224 (3), North Cay, Nassau, New Providence; UF 126226 (9), Delaport Point, New Providence; UF 126221 (2), Morgan's Bluff, Andros; UF 126234 (2), Frazier Hog Cay, Berry Islands; GTW 4265n (1), 1.0–2.5 m., Beachside, Chub Cay, Berry Islands; MW (2), Periwinkle Beach, Chub Cay, Berry Islands; HGL (1), Cat Island; HGL (2), Current, Eleuthera; MW (2), 18.0 m, Cay Sal, Cuba: UF 80982 (12), UF 80995 (5), Santiago; UF 80993 (5), Jauco; UF 80983 (7), Varadero; UF 80994 (1), Baracao; UF 54955 (1), Guantánamo; UF 80992 (4), Gibara; UF 17997 (6), La Habaña. Dominican Republic: UF 239824 (2), Barahona. Cayman Islands: UF 28935 (4), Preston Bay, Little Cayman; UF 239823 (1), Cayman Turtle Farm, Grand Cayman; UF 126230 (1), Red Bay, Grand Cayman. Jamaica: UF 61025 (4); UF 80987 (10), Flag Point. Puerto Rico: UF 80988 (1), Fajardo; GTW 4265z (1), 0.3–1 m, Escambron, San Juan; GTW 4265aa (3), 0.3–1 m, Enrique, La Parguera; GTW 4265ab (3), 0.3–1 m, Collao, La Parguera; GTW 4265ac (3), 0.3–1 m, Playa Buye, La Parguera; GTW 4265ad (7), 0.3–1 m, Media la Luna, La Parguera; GTW 4265ae (4), 1–3 m, El Corral, La Parguera; MW (3), Piñones Beach; HGL (7), Playa de Sardinera. U.S. Virgin Islands: UF 37856 (2), UF 80979 (43), Water Island; MW (3), 1 m, St. Croix; MW (1), 1 m, Ham Bay, St. Croix; UF 126216, St. Croix [7 paratypes of *Engina turbinella cruzana* (Nowell-Usticke, 1959)]. British Virgin Islands: UF 163643 (9), Tortola; KF 3929 (1), HGL (2), beached, Beef Island; HGL (3), 0.6 m, Buck Island; UF 163644 (4), Guana Island. Antigua: UF 80977 (3), UF 126235 (7); UF 120786 (2), Curtain Bluff; GTW 4265ai (5), 0.3–1 m, Long Bay; GTW 4265aj (2), 0.3–1 m, Deep Bay; GTW 4265ak (8), 0.3–1 m, Morris Bay; GTW 4265al (1), 0.3–1 m, Valley Church Bay; GTW 4265am (2), 0.3–1 m, Half Moon Bay; GTW 4265an (2), 0.3–1 m, Valley Church Bay; GTW 4265ao (1), 0.3–1 m, Cades Bay. Grenadines: EFG (1), 18 m, Montexuma Shoals, Mustique Island; KF 2503 (3), 12 m, St. Vincent, S end of Baliceaux Island; KF 5262 (3), 12 m, Savan Island; KF 2551 (1), 8–9 m, Cannoun Island. Grenada: GTW 4265t (12), GTW 4265u (14), GTW 4265v (8), GTW 4265w (4), GTW 4265x (7), GTW 4265y (2), 0.6–1.8 m, Coral Cove, Mt. Hartman Bay. Barbados: UF 80976 (2); UF 126220 (23), Hasting's Rock. Tobago: UF 70391 (3); UF 80980 (25); UF 126225 (6), UF 126237 (6), Buccoo Reef; UF 281378 (6), Friendship Beach; UF 281377 (7), UF 352067 (2), Scarborough; MW (2), Lambeau; MW (3), Irvine Bay. Mexico: EFG 26687 (1), 46–48 m, Campeche State, 22° 10.80' N, -91° 09.00' W; UF 383287 (4), Punta Hogna, Quintana Roo State; UF 264023 (1), Cayos Lobos, Quintana Roo State; UF 38338 (3), Cozumel, Quintana Roo State. Belize: GTW 4265c (4), 1 m, Sandbur Reef, Ambergris Caye; GTW 4265d (1), 1.5 m, Tres Cocos, Ambergris Caye; GTW 4265e (2), 0.3–1.5 m, Punta Robles, Ambergris Caye. Honduras: EFG 7365 (9), MW (2), Caribe Point, Isla Roatán; HGL (1), 0.5–1.3 m, Isla Roatán; GTW 4265g (1), 0.3–1.5 m, West Lime Key, SE Isla Roatán; GTW 4265h (1), GTW 4265i (2), GTW 4265j (1), 0.3–1.5 m,

Long Reef, Isla Roatán; GTW 4265k (6), SE Isla Roatán; GTW 4265l (1), 1–1.5 m, Old Port Royal, Isla Roatán; GTW 4265m (2), 1–1.5 m, Horseshoe Reef, Isla Roatán; HGL (5), Oak Ridge, Isla Roatán; KF 2173 (1), shallow water, Cayos Cochinos; KF 4141 (2), 2 m, Isla de Utila; MW (3), intertidal, Isla de Utila; HGL (19), Isla de Utila; UF 380423 (2), Guanaja; MW (2), 1 m, Guanaja. Costa Rica: UF 163876 (1), Punta Cahuita. Panama: UF 126217 (10), Colón; UF 80981 (9), UF 80989 (7), UF 160525 (2), Galeta Point; UF 80990 (2), Bocas del Toro; UF 160524 (3), Careening Cay, Bocas del Toro; UF 80991 (3), Devil's Beach; KF 3593 (2), Tiger Island; EFG 25590 (2), Isla Colón; UF 70393 (4), Bruja Point. Colombia: KF 3590 (3), Santa Marta; EFG 19507 (5), EFG 19508 (1), Isla de Providencia; EFG 25673 (1), Bocas del Toro. Venezuela: GTW 4265b (1), 7.3 m, Isla Morro Pelotas; GTW 4265ag (3), 2–5 m, Isla la Tortuga; HGL (5), Playa de Carenero; MW (1), Piedras Negras, Paraguaná Peninsula; MW (2), Isla de Margarita; MW (3), El Tunal, Isla de Margarita; EFG 19264 (1), Isla Borracha; KF 4735 (1), Punta San Juan. Netherlands Antilles: UF 80984 (2), UF 163642 (7), Bonaire; MW (6), 1.2 m, Kralendijk, Bonaire; UF 80986 (2), Aruba; UF 126245 (2), Palm Beach, Aruba. Brazil: GTW 4265af (1), 1–2 m, Buraco da Rachel, Fernando de Noronha; KF 78 (12), low tide, Fernando de Noronha.

**Distribution:** Widely distributed in southern Florida, rarely in the northern Gulf of Mexico, throughout the Bahamas, the Greater and Lesser Antilles, and along the Central American and northern South American coasts. Massemin et al. (2009) recorded this species from îles du Salut, French Guiana. Daccarett and Bossio (2011) recorded it from most of the Colombian Caribbean coast. Perhaps the strangest aspect of this species' distribution is its occurrence on Fernando de Noronha, 2,400 km away from the next known site in French Guiana, where it co-occurs with *E. demani*. Tryon (1881) recorded *E. elegans* from Sierra Leone but it is not listed by Ardonini and Cossignani (2004) and this record is probably in error.

**Habitat:** A shallow water species found from the intertidal zone to ca. 20 m. It seems to occur in deeper water off Florida and the northern Gulf of Mexico than elsewhere in the Caribbean. It is most commonly found under slabs of coral rubble, often in pairs, often almost completely covered in a thick, coralline algal deposit.

**Variation in Specimens:** Specimens vary greatly in size and degree of "fusiformity," but are relatively uniform in sculpture and, with few exceptions, coloration. All specimens have a peripheral band of white spots on the axial cords that may merge into a single unbroken band. In some populations the single spiral cord on the sub-sutural plane and/or the spiral cords anterior to the periphery may have white nodes as well. The two posterior-most outer lip denticles are almost always fused into a single large tooth. In the southeastern populations some specimens are an orange color (see discussion below) with numerous white spots. Specimens from the

Bahamas and the Lesser Antilles tend to be smaller than elsewhere, but there are numerous exceptions.

**Etymology:** *Engina turbinella* (Kiener, 1836): Latin, diminutive of *turbina*, a top. *Engina elegans* Gray, 1839: Latin, elegant. *Engina zonata* Gray, 1839: Latin, banded. *Engina turbinella cruzana* Nowell-Usticke, 1959: Spanish, *cruz* (cross), from the original name given by Christopher Columbus to the island of St. Croix, Santa Cruz.

**Comparison with Other Species:** The combination of a uniformly dark background color with white spots or bands, fused outer lip teeth, and dark aperture with white teeth characterize this species. Some specimens are similar to the Brazilian *E. permixta*; that is a relatively larger species with fewer axial ribs on both the final whorl (8–13 in *E. turbinella*, 7–10 in *E. permixta*) and the penultimate whorl (9–14 in *E. turbinella*, 8–10 in *E. permixta*). *Engina turbinella* never shows the wide range of colors seen in *E. permixta*. See Table 1 for a comparison with other species.

**Discussion:** *Engina turbinella* (Kiener, 1836) is a widespread and usually shallow water species occurring throughout much of the tropical western Atlantic Ocean. It is a baffling species varying greatly in size, shape, and coloration. Three color forms are apparent, all named, that appear rather distinct unless a large number of specimens is studied. These are discussed below.

*Purpura turbinella* Kiener, 1836. Louis Charles Kiener curated the vast (150,000 specimens) collection of Baron Jules Paul Benjamin Delessert, describing and illustrating many species in his *Spécies Général* (Dance, 1966). This included the "jolie petite espèce" *Purpura turbinella* from an unknown habitat, originally from the Prince Masséna collection, which Delessert had acquired in 1840. Subsequently this name has been almost universally applied to all western Atlantic *Engina* taxa as "*Engina turbinella*." Although the type is apparently lost, the illustrations (Figure 69) clearly show an orange shell with small white nodules above and below the usual peripheral row of nodules. This is not the widely distributed typical form illustrated in most accounts as *Engina turbinella*. Kiener's illustrations match our specimens from Scarborough, Tobago (Figures 70, 71). Although the size of the figured type specimen - "7 lig[nes]" [= 15.8 mm] is larger than the largest specimen we have seen from there (12.3 mm), given the great variation in size among other Caribbean *Engina* species we do not feel this is significant. These specimens represent a morph that appears to have a rather limited distribution from Barbados and Tobago to adjacent western Venezuela, including the Netherlands Antilles. It should be noted that orange shells occasionally are seen throughout the remainder of the western Atlantic Ocean and that shells may fade to an orange or tan color as well.

*Engina zonata* Gray, 1839. Tomlin (1928) mentioned a tablet at NHMUK labeled "*Enzina* [sic] *zonata* Gray. B.V. 113" with two examples. He misidentified them as *Engina leucozona* (Philippi, 1844) from the Mediterranean Sea.

Orr (1962) quoted Tomlin as saying the specimens represent “a possible type lot” but this phrase does not appear in his 1928 paper. Bartsch (1931) did not pick a lectotype of *zonata*, but simply illustrated one of the two specimens as the genotype of *Engina* without further comment. Orr (1962) selected and illustrated a lectotype from the same lot that Tomlin saw. Gray (1839) greatly mis-represented the size of the specimen as 1.5 inches long, a fact apparently overlooked by Bartsch (1931) but noted by Orr (1962). Tryon (1883: 196) also commented on *Engina zonata*: “This is also a lost species.” But types exist and prove to be *E. turbinella*. This is the morph most commonly found throughout the western Atlantic, where it insensibly grades into the other *E. turbinella* morphs described here. It is often quite large, particularly in populations off Miami and Panamá. Like the *E. turbinella* morph described above it usually has small, white nodules below the periphery (not apparent on the lectotype but visible on the paralectotype of *E. zonata*) but lacks the white sub-sutural nodules.

*Engina elegans* Gray, 1839 (and *Engina turbinella cruzana* Nowell-Usticke, 1959). This is the morph usually associated with the Greater Antilles and the Bahamas. It is often quite small in comparison to the *E. zonata* morph and usually lacks the sub-peripheral white nodules.

Examination of over 900 specimens indicates that these three morphs seem to blend from one to the other without clear-cut distinctions. Thus we prefer to recognize only the single species, *E. turbinella*. However, phylogenetic work may yet separate this “species” into two or more potentially cryptic species. The southeastern Caribbean form, the basis of the name *Purpura turbinella* Kiener, 1836, in particular seems the most morphologically and zoogeographically distinct of the three morphs. A peculiar form from the Grenadines (Figure 101) may represent a distinct species as well.

This is the only extant *Engina* species from the western Atlantic with a fossil record. It was recognized from the middle Miocene of Panamá by Woodring (1973) and the late Pleistocene of the Dominican Republic by Landau and Vermeij (2012).

#### *Engina williamsae* new species (Figures 13, 103–107)

**Description (based on 11 adult specimens):** Largest specimen, 15.0 mm in length; smallest specimen, 11.5 mm in length; holotype 12.6 in length  $\times$  7.4 mm in width. Spire occupies 60% of total length. Protoconch minute, of 1.5 smooth whorls, white with tan patches or bands. Teleoconch of ca. 5 whorls. Spiral sculpture consists of a wide subsutural slope with a narrow primary thread with microscopic secondary threads; the periphery has 4 indistinct primary cords over the axial nodes and microscopic threads; anteriorly there are 5 wide, flat primary cords separated by deeply incised channels. Axial sculpture of numerous microscopic threads on sub-sutural band and 8–10 (mode=9) elongated primary peripheral nodes on the final whorl, 9–10 (mode=9) on

penultimate whorl. Terminal varix only slightly more developed than previous axial sculpture. Aperture small, constricted. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 5–6 (mode=5) semi-lirate denticles, the anterior-most forming a weak, long, thin rib that projects deep into the aperture and delimits the siphonal canal, barely perceptible in some specimens. Radial lirae (2–5, mode=5) at posterior end, weak and irregular. Anterior to these are columellar folds (2–6, mode=6), weak or absent from center of columella, often limited to edge of parietal wall, anterior-most two best-developed and forming a ridge on the interior of the columella. Background color white, subsutural slope gray, wide brown blotches on the subsutural slope and between the axial ribs on the posterior half, leaving a white sub-peripheral band, anteriorly colored with brown spots, more or less aligned axially. Aperture pale tan. Operculum rounded, leaf-shaped, yellow with brown central radius. Radula and anatomy unknown.

**Holotype:** UF 478947 (ex MW).

**Type Locality:** 15 m, off Egmont Key, Hillsborough Co., Florida, USA.

**Paratype(s):** UF 478946 (1), 15 m, off Egmont Key, Hillsborough Co., Florida, USA (ex MW); BMSM 75998 (1), off Egmont Key, Hillsborough Co., Florida, USA (ex MW).

**Other Material Examined (9 specimens):** Western Florida: UF 239809 (1), 220 m, off Egmont Key, Hillsborough Co.; HGL (2), MW (4), 15 m, off Egmont Key, Hillsborough Co.; MW (1), 14 m, off Egmont Key, Hillsborough Co.; MW (1), 14 m, off Anna Maria Island, Manatee Co.

**Distribution:** Known only from off Egmont Key and adjacent Anna Maria Island, Hillsborough and Manatee counties, Florida, Gulf of Mexico.

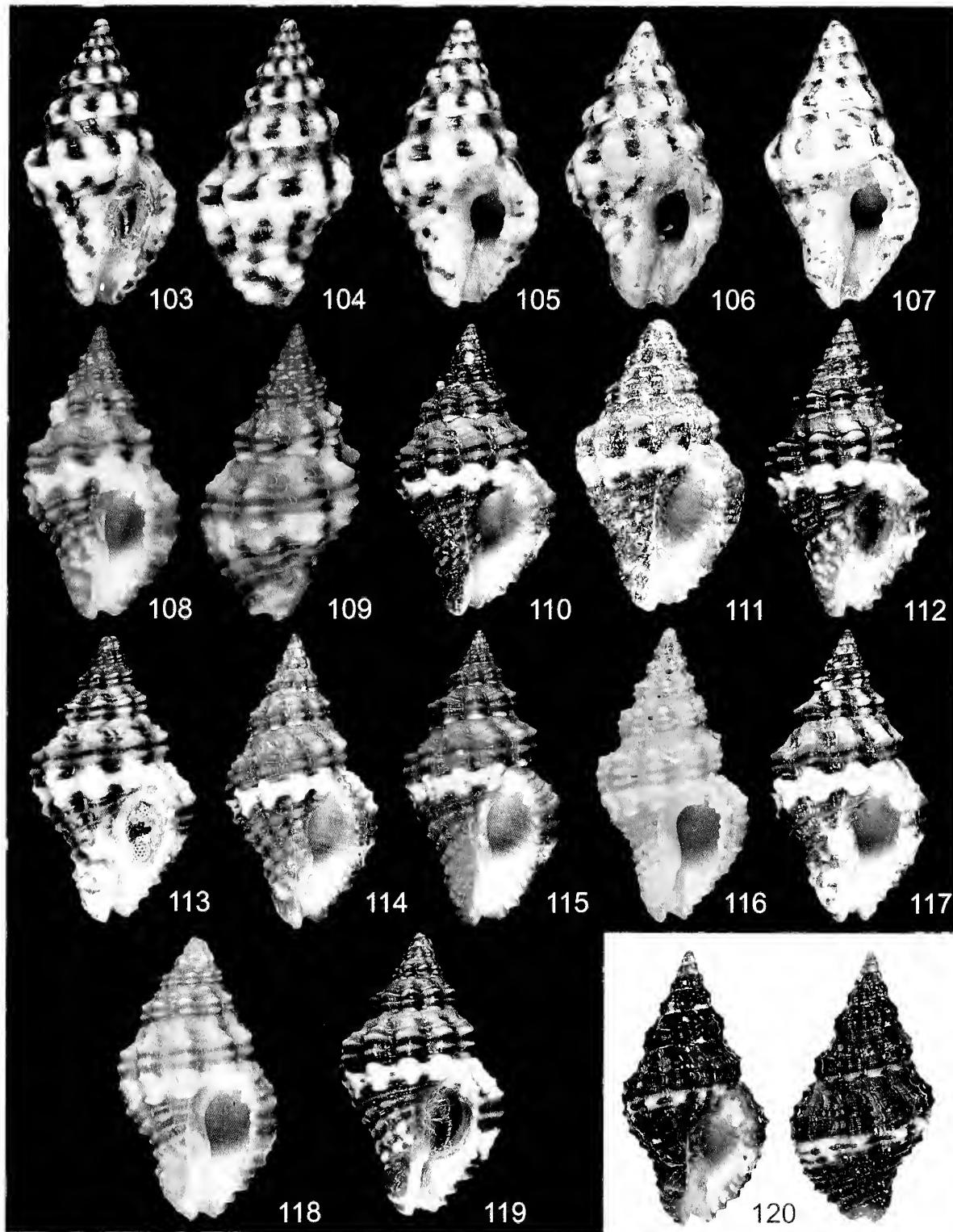
**Habitat:** Live and dead specimens collected on rock reef in 15 m. Other specimens known to 220 m.

**Variation in Specimens:** The few known specimens are remarkably uniform in coloration and sculpture.

**Etymology:** Named for Margaret “Peggy” Williams of Tallavast, Florida, who collected most of the known examples.

**Comparison with Other Species:** This species is similar to *E. corinnae*. That species has more prominent spiral sculpture over the entire shell, including the sub-sutural band, which is nearly smooth in *E. williamsae*. See Table 1 for a comparison with other species.

**Discussion:** *Engina williamsae* is only known from Egmont Key and Anna Maria Island off the Gulf coast of Florida. These sites are at the mouth of Tampa Bay, a large open-water estuary. It has not yet been found on



**Figures 103–120.** *Engina* species. **103–107.** *Engina williamsae* new species. **103–104.** Holotype, UF 478947, 14.5 mm. **105.** Paratype, BMSM 75998, 13.0 mm. **106.** Paratype, UF 479946, 15.0 mm. **107.** MW, 13.6 mm. All specimens from 15 m, off Egmont Key, Hillsborough Co., Florida. **108–119.** *Hesperisternia karinæ* (Nowell-Usticke, 1959). **108–109.** Holotype, AMNH 193771, 23 mm. **110.** KF 2505, 5–7 m, Ronde Island, Grenada, 18.5 mm. **111.** HGL, 9.1 m, Pickles Reef, Monroe Co., Florida, 19.9 mm. **112.** HGL, 201 m, St. Anne, Guadeloupe, 19.8 mm. **113.** GTW 6613c, 20–25 m, off Guarapari, Espírito Santo State, Brazil, 21.0 mm. **114.** GTW 6613a, 6.1 m, Tambor Cay, Panamá, 18.5 mm. **115.** GTW 6613e, French Guiana, 17.1 mm. **116.** GTW 6613b, 12 m, off Guarapari, Espírito Santo State, Brazil, 21.9 mm. **117.** KF 4535, Isla Los Aves, Venezuela, 19.3 mm. **118.** HGL, Playa de Ponce, Puerto Rico, 21.1 mm. **119.** KF 2947, Port Louis, Guadeloupe, 20.8 mm. **120.** *Hesperisternia* sp., GTW 6613d, Amuay, Venezuela, 18.8 mm.

adjacent Mullet and Sister keys. Given the amount of recreational shelling that takes place in the area it is surprising that more examples have not been found. Most specimens are worn and crabbed.

### ***Hesperisternia* Gardner, 1944**

**Type Species:** *Hesperisternia waltonia* Gardner, 1944, by original designation.

**Discussion:** In *Hesperisternia* the lirae extend much further back within the aperture than in *Engina*. Vermeij (2006) reviewed the fossil and Recent species. Additional notes are given here for *Hesperisternia karinae* (Nowell-Usticke, 1959) because it occupies a much larger range than is usually thought and is often misidentified in collections. It is redescribed and its distribution is given so that its proper place in the western Atlantic fauna may become more clear.

In addition to *H. karinae*, other western Atlantic Ocean Recent taxa include *Hesperisternia multangula* (Philippi, 1848) and *Hesperisternia harasewychi* (Petuch, 1987). Abbott (1986) named a subspecies, *H. multangula grandana*, which Vermeij (2006) considered a minor variant, but which Petuch (2013) raised to a full species. *Hesperisternia itzamnai* Watters, 2009, and *Engina janowskyi*, placed in *Hesperisternia* by Watters (2009), are reallocated to *Engina* based on the study of Landau and Vermeij (2012). An additional undescribed *Hesperisternia* occurs at Amuay, Venezuela, but it is only known to us from a single specimen (Figure 120).

### ***Hesperisternia karinae* (Nowell-Usticke, 1959)** (Figures 68, 108–119)

*Tritonidea orbignyi* Payraudeau, 1826. Dall and Simpson, 1901: 400 [misidentification].

*Cantharus karinae* Nowell-Usticke, 1959: 69, pl. 4, fig. 4; Warmke and Abbott, 1961: 118 [in synonymy of *Cantharus laetus* Reeve, 1846]; Nowell-Usticke, 1969: 17, pl. 4, fig. 4; Nowell-Usticke, 1971: 13–14, pl. 2; Leal, 1991: 153, pl. 19, fig. G.

non *Cantharus laetus* Reeve, 1846. — Warmke and Abbott, 1961: 118, pl. 21, fig. c [misidentification].

*Pisania karinae* (Nowell-Usticke, 1959). — Kaicher, 1986: card 4370; de Jong and Coomans, 1988: 84.

*Hesperisternia karinae* (Nowell-Usticke, 1969 [sic]). — Vermeij, 2006: 81.

*Hesperisternia karinae* (Nowell-Usticke, 1953 [sic]). — Watters, 2009: 271.

**Description (based on 19 adult specimens):** Largest adult specimen, 25.0 mm in length; smallest specimen, 17.0 mm in length. Spire occupies 50% of total length. Protoconch minute, of 1.5 smooth whorls, tan with a brown band. Teleoconch of ca. 6.25 whorls. Spiral sculpture of 10–13 (mode =12) primary ribs, usually absent from the sub-sutural ramp, between which are single secondary threads flanked by a few tertiary threads. Axial sculpture of large primary ribs, absent or

greatly reduced on the subsutural slope, most developed at the periphery; 6–8 (mode=7) on both the last whorl and on the penultimate whorl. Intersections of axial and spiral sculpture form elongated spiral pustules on the primary spiral cords. Terminal varix only slightly more developed than previous axial sculpture. Aperture oval, constricted. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 8–10 (mode=10) lirate denticles, in all but the anterior two, which are quite short, the lirae curve back deep into the aperture. The long, thin rib that projects deep into the aperture and delimits the siphonal canal in some *Engina* is not present. Radial lirae at posterior end composed of combinations of 4–10 pustules and irregular lirae, often mixed together. Anterior to these are columellar folds (8–10, mode=10) posteriorly composed of irregular pustules, anterior 2–3 folds of long lirae. Interior ledge of columella well-developed. Background color yellow or tan with a prominent, wide, undulating, white peripheral band. This band is often bounded on each side by a thin dark brown line and may have dark brown flecks embedded within it. A diffuse, broad, dark band occurs above and below the white peripheral band. Subsutural slope and pustules lighter in color – yellow or tan. Aperture white, columella showing through to brown below. Operculum rounded, leaf-shaped, yellow with brown central radius. Radula and anatomy unknown. Leal (1991) figured the protoconch.

**Holotype:** AMNH 193771.

**Type Locality:** N of Fredericksted, [St. Croix, US Virgin Islands].

**Paratype(s):** AMNH 294356 (1); UF 154704 (1); both from the type locality.

**Other Material Examined (35 specimens):** Florida: UF 352842 (1), UF 352843 (1), dredged off Delray Beach, Palm Beach Co.; UF 126511 (1), 27 m, off Palm Beach Inlet, Palm Beach Co.; UF 126510 (1), 37 m, off Palm Beach, Palm Beach Co.; UF 157523 (4), 18 m, Pompano Beach, Broward Co.; UF 398301 (1), 365.8 m, off Hillsboro, Broward Co.; HGL (1), 9 m, off Pickles Reef, Key Largo, Monroe Co. Bahamas: UF 168507 (1), Cat Cay, Bimini. Puerto Rico: UF 162628 (1), Córcega Beach, Rincón; UF 162629 (1), Rincón; HGL (3), Playa de Ponce. U.S. Virgin Islands: UF 154704 (1), N of Fredericksted, St. Croix [paratype]. Guadeloupe: HGL (3), 201 m, St. Anne; KF 2947 (4), Port Louis, Grenada: KF 2505 (1), 5–7 m, Ronde Island. Panama: GTW 6613a (1), 6 m, Tambor Cay. Venezuela: KF 4535 (1), Isla Los Aves. French Guiana: GTW 6613e (1). Brazil: HGL (1), 6 m, Salvador, Bahia State; HGL (1), 10–12 m, Salvador, Bahia State; HGL (1), off Guarapari, Espírito Santo State; GTW 6613c (2), 20–25 m, off Guarapari, Espírito Santo State; GTW 6613b (2), 12 m, off Guarapari, Espírito Santo State.

**Distribution:** This is a rare but widely distributed species: southeastern Florida, sporadically throughout the eastern Caribbean to Espírito Santo State, Brazil, but with considerable gaps in this distribution. It has not been recorded from Central America beyond Panamá, or from Cuba or Hispaniola, although it probably occurs there. It was not included as part of the North American fauna by Abbott (1974). Recorded by Dall and Simpson (1901) from Ponce and Culebra, Puerto Rico, as *Tritonidea orbignyi* Payraudeau, 1826. Nowell-Usticke (1971) added Antigua, Barbados, Grenada, Curaçao, and Aruba to his original description. Leal (1991) recorded it from Trindade and Vitória seamounts.

**Habitat:** Live and dead individuals have been found from 6–366 m. It appears to live in shallower water in the southern Caribbean than in the northern part of its range. It has been found on calcareous rubble.

**Variation in Specimens:** The degree of development of the axial sculpture varies considerably. The overall coloration varies from yellowish to a mahogany color but the wide, white peripheral band is always present.

**Etymology:** Named after Nowell-Usticke's wife, Karin.

**Comparison with Other Species:** This relatively large and brightly colored species should not be confused with any other species from the western Atlantic. No species of *Engina* from there has a similar color pattern, or the elongate, lirate outer lip denticles, or the pustulose radial lirae. See Table 1 for a comparison with other species.

**Discussion:** This species has been identified in most collections as *Buccinum lautm* Reeve, 1846, described from an unknown locality. That species is the eastern Pacific taxon *Gemophos laetus* (Reeve, 1846).

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# On two abyssal species of Scaphandridae G.O. Sars, 1878 (Gastropoda: Cephalaspidea) from the eastern Pacific

Ángel Valdés

Department of Biological Sciences  
California State Polytechnic University  
3801 West Temple Avenue  
Pomona, CA 91768 USA  
Email: aavaldes@cpp.edu

James H. McLean

Natural History Museum of Los Angeles County  
900 Exposition Boulevard  
Los Angeles, CA 90007 USA  
Email: jmclean@nhm.org

## ABSTRACT

*Scaphander interruptus* Dall, 1890 is a widespread, deep-water eastern Pacific species whose range is extended to California. The anatomical features of this species are similar to those of other members of *Scaphander* de Monfort, 1810, including the presence of a single lateral tooth on each half-row of the radula and the morphology of the penial complex. Another eastern Pacific species, *S. cylindrellus* Dall, 1908 is reassigned to the genus *Cyllichnium* Dall, 1908 because of the presence of a multidenticulate radula, a female copulatory organ and its shell morphology.

**Additional Keywords:** *Scaphander*, *Cyllichnium*, Panamic, deep sea, redescriptions.

## INTRODUCTION

The family Scaphandridae, recently resurrected by Malaquias et al. (2009), is poorly known in the eastern Pacific, particularly in the deep sea. Two species are problematic and in need of revision. A review of the literature and material collected from several localities has raised doubts about the taxonomic placement of *Scaphander cylindrellus* Dall, 1908. Newly collected material of *Scaphander interruptus* Dall, 1890 showed a previously unrecorded variability in shell morphology and has allowed for anatomical studies. The present paper deals with these two species and attempts to place them taxonomically in light of recent studies on the systematics of Scaphandridae (Valdés 2008; Malaquias et al. 2009; Eilertsen and Malaquias, 2013a). Additionally, new information on their morphological variability, range, and internal anatomy is provided.

## MATERIALS AND METHODS

The material examined is deposited at the Natural History Museum of Los Angeles County (LACM), the Department of Invertebrate Zoology and Geology at the California

Academy of Sciences, San Francisco (CASIZ), the Benthic Invertebrate Collection of the Scripps Institution of Oceanography (SIO), and the National Museum of Natural History (USNM). The material is noted here as “shell” for empty shells and “specimen” for complete specimens including shell and soft parts. The material was unsuitable for molecular work.

The specimens were dissected for examination of the reproductive and digestive system anatomy. The reproductive anatomy was examined under a Nikon SMZ-100 dissecting microscope and drawn with the aid of a *camera lucida*. The gizzard plates and radulae were isolated from surrounding tissue by submerging them in NaOH 10%, then rinsed in water, dried and examined under a Cambridge 360 Scanning Electron Microscope at the University of Southern California Center for Electron Microscopy and Microanalysis.

## SYSTEMATICS

### Genus *Scaphander* de Monfort, 1810

**Type Species:** *Bulla lignaria* Linnaeus, 1758 (Mediterranean and northeastern Atlantic), by original designation.

*Scaphander* de Monfort, 1808–10 [1810]: 334.

**Diagnosis:** Shell external, oblong, tapered posteriorly, with the spire concealed by callus and covered with a thin periostracum. Microsculpture consisting of spiral lines or series of pits. Aperture as long as the shell, narrow above, much wider below. Radula with single, hamate lateral teeth. Rachidian teeth generally absent, a vestigial rachidian tooth present in several species. Reproductive system monaulic. Penis unarmed, connected to the prostate by a long duct. Gizzard with two large, paired kidney-shape to sub-triangular plates and an unpaired thin, elongate plate.

**Remarks:** *Scaphander* is a genus of predominantly deep-sea cephalaspidean sea slugs, with species distributed

worldwide from the Arctic to the Antarctic (Eilertsen and Malaquias, 2013a). The shell morphology and anatomy of *S. lignarius* (Linnaeus, 1758), the type species, have been summarized and illustrated by Thompson (1976) and by Eilertsen and Malaquias (2013a). Eilertsen and Malaquias (2013a) provided the first molecular phylogeny for this group including Atlantic and Western Pacific species, and Eilertsen and Malaquias (2013b) examined the digestive system morphology and diet of this group.

### **Scaphander interruptus Dall, 1890 (Figures 1–10)**

*Scaphander interruptus* Dall, 1890: 297, pl. 12, fig. 12. Dall, 1908: 239.

**Shell Morphology:** Shell up to 22 mm in length and 11 mm in width (LACM 73-109), involute, oval (Figure 1). Aperture as long as the shell, wider anteriorly and constricted posteriorly. Lip rising slightly above the apex (Figures 1, 6, 7). The sculpture consists of spiral lines of oval pits, with alternating rows of wider and narrower pits (Figure 2).

**Digestive System:** The buccal mass is small and connects dorsally with the esophagus and the salivary glands (Figure 10). At its posterior end two strong retractor muscles attach. The esophagus opens into a large muscular gizzard, which contains three gizzard plates. Two of the gizzard plates are large and oval (Figure 3), whereas the third one is elongate (Figure 4). The radular formula is  $12 \times 1.0.1$  ( $n = 1$ ). Lateral teeth are hamate, with a number of small denticles (Figure 5).

**Reproductive System:** The reproductive system is monaulic, but the female parts of the reproductive system were not seen. The penial complex consists of a bulbous, muscular penis and an oval prostate connected to the penis by an elongate duct (Figure 9).

**Material Examined:** CALIFORNIA (all specimens collected by K. L. Smith, R/V NEW HORIZON), approximately 226 km west of Point Arguello, Santa Barbara County ( $34^{\circ}44' N$ ,  $123^{\circ}07' W$ ), 4100 m depth, 1 fragment of shell, 22 July 1991 (LACM 91-130.2); ( $34^{\circ}43' N$ ,  $123^{\circ}07' W$ ), 4100 m depth, 1 broken shell, 1 August 1991 (LACM 91-131.3); ( $34^{\circ}45' N$ ,  $123^{\circ}04' W$ ), 4100 m depth, 1 specimen, dissected, 21 October 1991 (LACM 91-133.3); ( $34^{\circ}44' N$ ,  $123^{\circ}12' W$ ), 4100 m depth, 1 fragment of shell, 4 November 1993 (LACM 93-74.1); ( $34^{\circ}42' N$ ,  $123^{\circ}08' W$ ), 4100 m depth, 1 fragment of shell, 7 November 1993 (LACM 93-75.2); ( $34^{\circ}43' N$ ,  $123^{\circ}14' W$ ), 4100 m depth, 1 shell, 12 October 1996 (LACM 1996-85.3). COSTA RICA, 14 miles from Punta Guiones ( $9^{\circ}45'18'' N$ ,  $85^{\circ}52'24'' W$ ), 12 May 1973, 1866 m depth, 1 shell, leg. R/V VELERO IV (stn. 18932) (LACM 73-109). PERU, West of Isla Lobos de Tierra ( $6^{\circ}26' S$ ,  $81^{\circ}05' W$ ), 1025 m depth, 1 shell, leg. McLean and Del Solar, 23 January 1974 (LACM 74-18). CHILE:

R/V USS ALBATROSS Expedition, station 2788, west coast of Chile ( $45^{\circ}35' S$ ,  $75^{\circ}55' W$ ), 1050 fathoms (1920.24 m), 3 shells, 11 February 1888 (SYNTYPES, USNM 97075).

**Geographic Range:** This species was originally described from Chile. It is otherwise known from southern California, Baja California, Costa Rica, and Peru (present paper).

**Remarks:** *Scaphander interruptus* Dall, 1890 is the only species of the genus known from the eastern Pacific. Examination of the type series (Figure 6) confirms the identity of the material here studied as *S. interruptus*; the anatomical examinations conducted confirm the placement of this species in *Scaphander*. The radula, with a single lateral tooth, the presence of three gizzard plates, two of them larger, and the morphology of the penial complex (with a simple unarmed penis and a single unmodified prostate), are characteristics of this genus (Gosliner, 1994; Eilertsen and Malaquias, 2013a).

Keen (1971, fig. 2256) assigned a shell collected off Bahía Magdalena, Baja California, Mexico to *S. interruptus*. Examination of this specimen (Figure 8; CASIZ 156489) revealed some differences in shell morphology and sculpture with the other specimens of *S. interruptus* here studied. In typical specimens of *S. interruptus* the lip rises over the spire and the sculpture is composed of clearly visible oval pits, whereas the specimen from Bahía Magdalena has a shorter lip and the sculpture is not well marked. The specimen from Bahía Magdalena is here regarded as indeterminable.

### **Genus *Cylichnium* Dall, 1908**

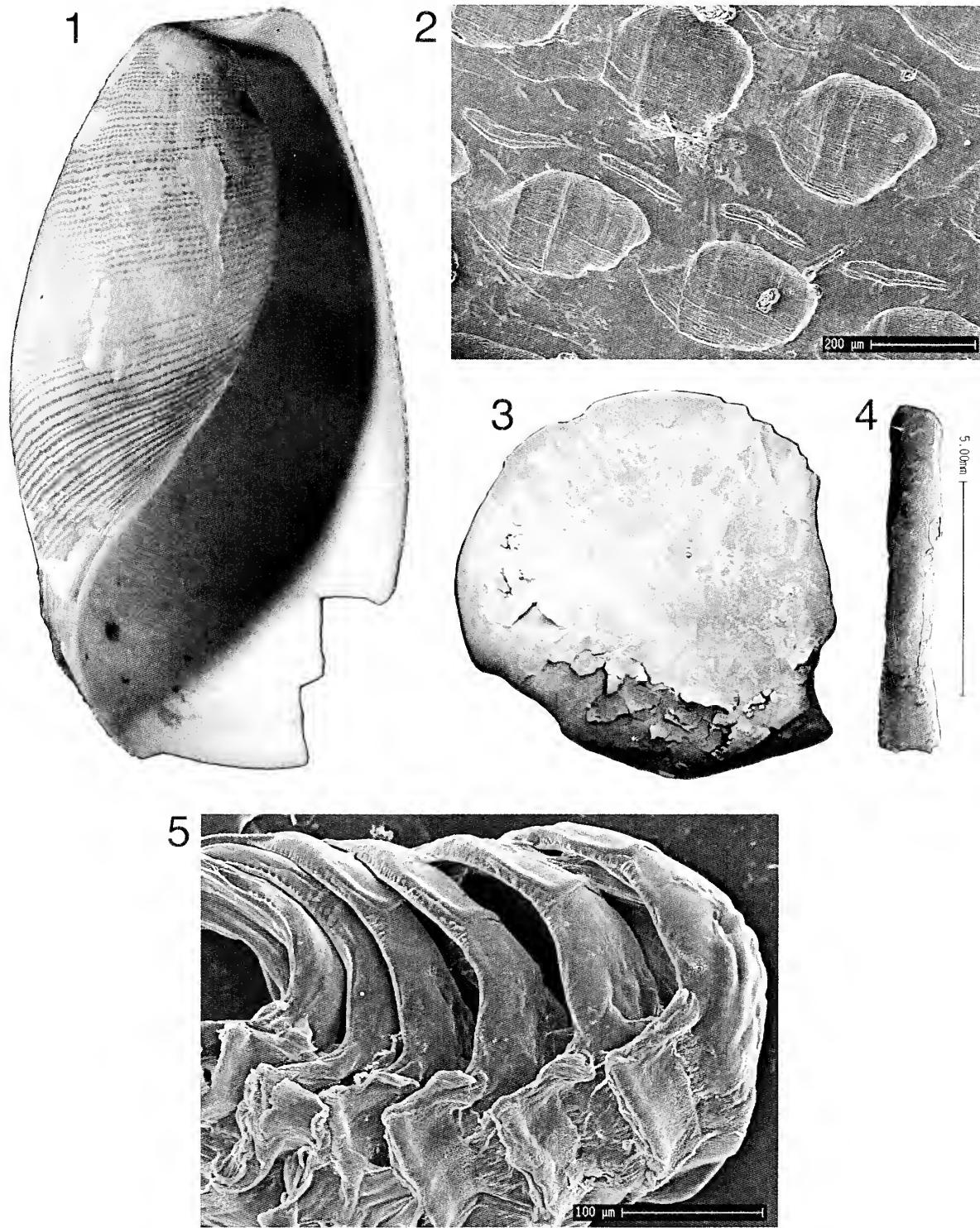
**Type Species:** *Utriculus domitus* Dall, 1889 (Caribbean), by original designation.

*Cylichnium* Dall, 1908: 242.

*Volvulopsis* Schepman, 1913: 463. Type species, by original designation: *Volvulopsis ancillariooides* Schepman, 1913 (Indonesia).

**Diagnosis:** Shell external, elongated-oval, with somewhat elevated or covered spire, in most cases with fine spiral lines. Aperture long, narrow above, wider below. Radula with several simple and hamate lateral teeth. Rachidian teeth absent. Reproductive system monaulic, with a complex female copulatory organ. Penis unarmed.

**Remarks:** The genus *Cylichnium* was originally described as a subgenus of *Cylichnella* Gabb, 1873, based on three species, *Utriculus domitus* Dall, 1889 (the type species by original designation), from Guadeloupe, *Cylichnella pizarro* Dall, 1908 from Panama, and *Cylichnella atahualpa* Dall, 1908 also from Panama (Dall, 1908). Subsequently, several other species were assigned to this genus: *C. matsumotoi* Habe, 1955 (from Japan), *C. waldae* Bouchet, 1975 (from the Atlantic), and *C. oliviformis* (Watson, 1883). Bouchet (1975) transferred *Aceras africana* Fischer in Locard, 1897 and its synonym *Aceras*



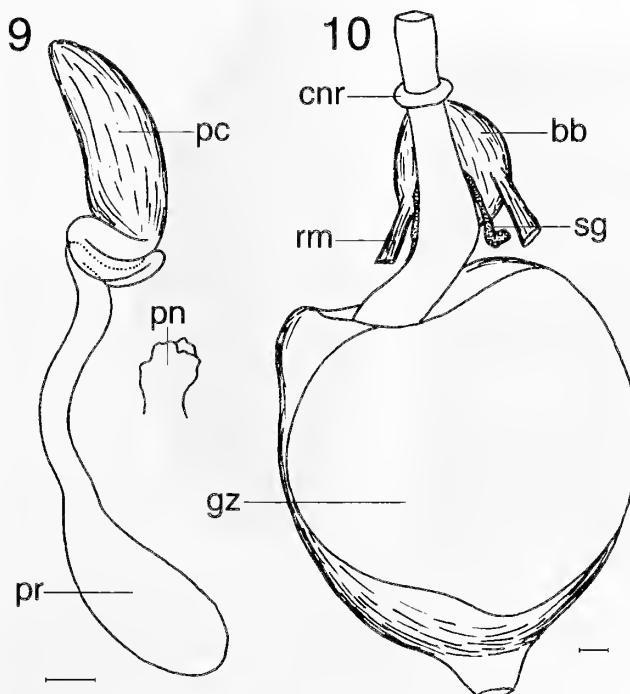
**Figures 1–5.** *Scaphander interruptus* Dall, 1890. 1. Costa Rica (LACM 73-109), shell length 24 mm. 2. SEM photograph of the shell microsculpture (LACM 91-133.3). 3, 4. SEM photographs of a gizzard plates (LACM 91-133.3). 5. Radular teeth (LACM 91-133.3).

*fischeri* Locard, 1897 to *Cyllichnium*, based on anatomical examination of newly collected specimens. A review of the original description of *Cyllichnium* shows that the type species (*U. dominus*) has a short, conical shell, with an aperture about 4/5 of the shell length and a pointed apex,

so it appears to be a juvenile specimen. On the other hand, the two Panamanian species *C. pizarro* and *C. atahualpa* are much smaller than other *Cyllichnium* and are most likely members of the genus *Cylchna* Lovén, 1846, as already suggested by Keen (1971). Valdés



**Figures 6–8.** *Scaphander interruptus* Dall, 1890. 6. Syntype (USNM 97075). 7. Specimen from Isla Lobos de Tiera, Peru (LACM 74-18), shell length 15 mm. 8. Indeterminable specimen assigned to *S. interruptus* by Keen (1971), collected off Bahía Magdalena, Baja California, Mexico (CASIZ 156489), shell length 12 mm.



**Figures 9–10.** *Scaphander interruptus* Dall, 1890, anatomy (LACM 91-133.3). 9. Penial complex; scale bar = 1 mm. 10. Anterior portion of the digestive system; scale bar = 1 mm. Abbreviations: **bb**, buccal bulb; **cnr**, circumesophageal nerve ring; **gz**, gizzard; **pc**, penal capsule; **pn**, penis; **pr**, prostate; **rm**, retractor muscle; **sg**, salivary gland.

(2008) described two additional species of *Cylichnium*, *C. mucronatum* Valdés, 2008 and *C. nanum* Valdés, 2008 from deep waters in the tropical Indo-Pacific, and synonymized *C. matsumotoi* Habe, 1955 and *C. sumatrense* Thiele, 1925 with *C. ancillarioides*.

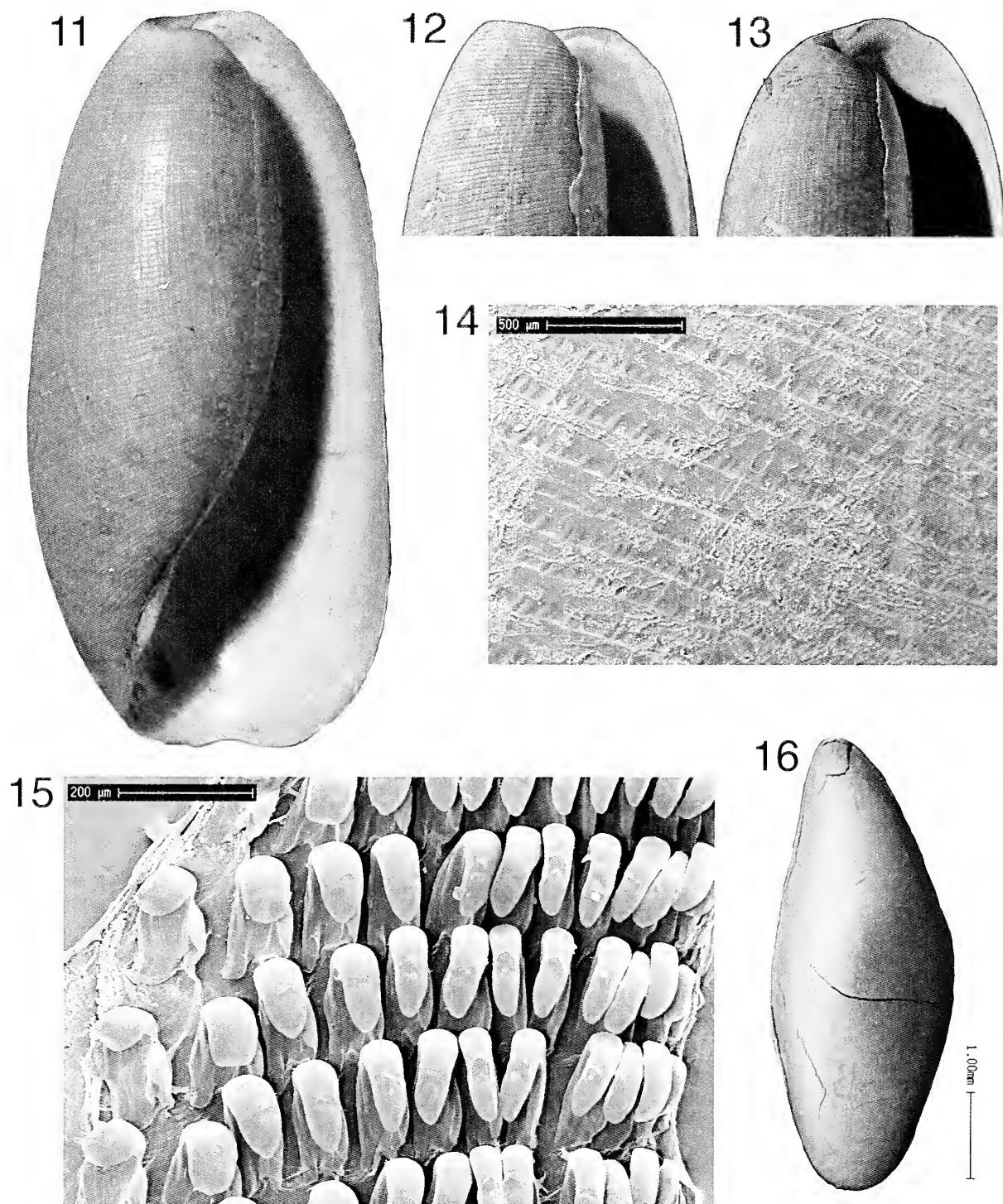
Schepman (1913) described the genus *Volvulopsis* based on the single species *V. ancillarioides* Schepman, 1913, from Indonesia (959–1301 m depth). Subsequent authors regarded *Volvulopsis* as a synonym of *Cylichnium* Dall, 1908 (see Bouchet, 1975; Valdés, 2008). The shell characteristics of *V. ancillarioides* resemble those of adult species assigned to *Cylichnium* by Habe (1955) and Bouchet (1975). *Cylichnium* differs from *Scaphander* in the presence of a female copulatory organ, wider radula with several lateral teeth and a narrower shell (Valdés, 2008).

Following these revisions, *Cylichnium* now contains six valid species [*C. dominus* (Dall, 1889), *C. africanum* (Fischer in Locard, 1897), *C. ancillarioides* (Schepman, 1913), *C. waldae* Bouchet, 1975, *C. mucronatum* Valdés, 2008 and *C. nanum* Valdés, 2008], all of them from deep waters in the tropical Indo-Pacific, Japan, the Caribbean, and the eastern Atlantic.

#### *Cylichnium cylindrellum* (Dall, 1908) (Figures 11–18)

*Scaphander cylindrellus* Dall, 1908: 239, pl. 8, fig. 1; Keen, 1971: 800, fig. 2255.

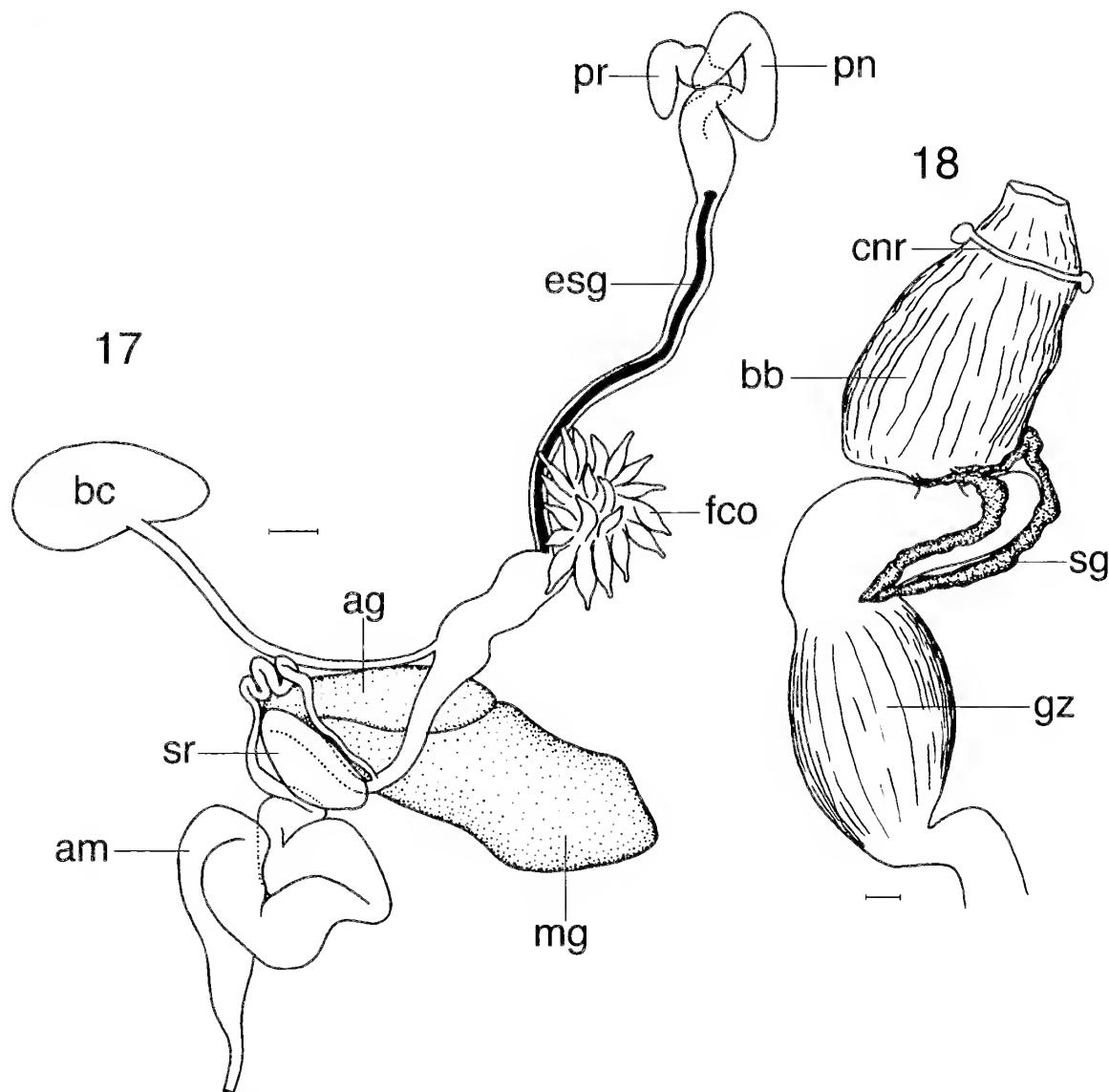
**Shell Morphology:** Shell 33 mm in length and 16 mm in diameter (holotype), somewhat cylindrical, with nearly parallel sides (Figure 11). Aperture as long as the shell,



**Figures 11–16.** *Cylichnium cylindrellum* (Dall, 1908). **11.** Holotype (USNM 110563), shell length 29 mm. **12.** Apex of a shell from Santa Barbara County, California (LACM 95-126.3). **13.** Apex of a shell from Bahía Magdalena, Baja California, Mexico (CASIZ 156490). **14.** SEM photograph of the shell microsculpture (LACM 94-58.3). **15.** Half-row of the radula (LACM 94-58.3). **16.** SEM photograph of a gizzard plate (LACM 94-58.3), showing several fractures produced as the consequence of the drying process for SEM examination.

wider anteriorly and constricted posteriorly. Apex sunken, convex. Lip raising above the apex in some specimens (Figures 11, 13), whereas in others the lip is lower than the apex (Figure 12). Sculpture with fine spiral grooves

crossed by microscopic axial lines only present in the spiral grooves (Figure 14). All specimens were preserved, so information on the external coloration and shape of the body is unavailable.



**Figures 17–18.** *Cyllichnium cylindrellum* (Dall, 1908), anatomy (LACM 94-58.3). **17.** Reproductive system; scale bar = 1 mm. **18.** Anterior portion of the digestive system; scale bar = 1 mm. Abbreviations: **am**, ampulla; **ag**, albumen gland; **bb**, buccal bulb; **bc**, bursa copulatrix; **cnr**, circumesophageal nerve ring; **esg**, external seminal groove; **fco**, female copulatory organ; **gz**, gizzard; **mg**, mucous gland; **pn**, penis; **pr**, prostate; **sg**, salivary gland; **sr**, seminal receptacle.

**Digestive System:** The buccal mass is large and heavily muscular (Figure 18). At its posterior end it connects to the esophagus and two elongate salivary glands. The esophagus is short and opens into the muscular gizzard, which contains three subequal gizzard plates. All three gizzard plates are oval and smooth (Figure 16). The radular formula is  $20 \times 12.0.12$  ( $n = 1$ ). All lateral teeth are hamate, with no denticulations (Figure 15). The innermost tooth of each row is wider than the outer lateral teeth and has a lateral prolongation on its outer edge.

**Reproductive System:** The reproductive system is monaulie (Figure 17). The ampulla is large and convoluted. It connects to the narrow and elongate post-ampullary

duct. The seminal receptacle enters the post-ampullary duct that continues distally to the common general atrium. Also entering the common atrium are the female glands and the bursa copulatrix (or gametolytic gland). From the gonophore an open seminal groove runs anteriorly to the protusible cephalic penis and the prostate. At the vaginal opening there is a complex female copulatory organ.

**Material Examined:** CALIFORNIA (all specimens collected by K. L. Smith, RV NEW HORIZON), approximately 226 km west of Point Arguello, Santa Barbara County ( $34^{\circ}44' N$ ,  $123^{\circ}11' W$ ), 4100 m depth, 1 specimen, 18 February 1990 (LACM 90-162.1); ( $34^{\circ}45' N$ ,  $123^{\circ}07' W$ ), 4100 m depth, 1 specimen, dissected, 24 June

1991 (LACM 91-41.1); (34°43' N, 123°07' W), 4100 m depth, 1 shell with dried soft parts, 2 August 1991 (LACM 91-132.4); (34°47' N, 123°04' W), 4100 m depth, 1 specimen, 26 February 1992 (LACM 92-109.1); (34°41' N, 123°03' W), 4134 m depth, 1 specimen, 25 June 1992 (LACM 92-111.1); (34°38' N, 120°01' W), 4134 m depth, 1 specimen, 22 July 1992 (LACM 92-112.1); (34°43' N, 123°04' W), 4100 m depth, 1 fragment of shell, 20 October 1992 (LACM 92-114.2); (34°45' N, 123°02' W), 4100 m depth, 1 fragment of shell, 24 February 1993 (LACM 93-21.10); (34°42' N, 123°08' W), 4100 m depth, 1 shell and a fragment of shell, 20 July 1993 (LACM 93-43.7); (34°39' N, 122°58' W), 4100 m depth, 2 fragments of shell, 17 June 1994 (LACM 94-58.10); 4100 m depth, 2 specimens, 17 June 1994 (LACM 94-58.3); (34°44' N, 123°13' W), 4100 m depth, 1 shell, 21 August 1994 (LACM 94-59); (34°42' N, 123°09' W), 4100 m depth, 1 shell and two fragments, 14 February 1995 (LACM 95-19.2); (34°42' N, 123°09' W), 4100 m depth, 1 specimen, 14 February 1995 (LACM 95-19.3); (34°42' N, 123°05' W), 4100 m depth, 1 specimen, 17 February 1995 (LACM 95-20.3); (34°40' N, 123°03' W), 4100 m depth, 1 fragment of shell, 1 May 1995 (LACM 95-21.9); (34°40' N, 123°03' W), 4100 m depth, 1 specimen, 1 May 1995 (LACM 95-21.8); (34°40' N, 123°11' W), 4100 m depth, 1 specimen, 3 June 1995 (LACM 95-126.3); (34°40' N, 123°11' W), 4100 m depth, 2 specimens, 31 May 1996 (LACM 96-38.1); (34°40' N, 123°11' W), 4100 m depth, 1 fragment, 5 June 1996 (LACM 96-39.8); (34°41.710' N, 123°12.570' W), 4110 m depth, 2 August 2004, 1 fragment of shell (SIO M11388); (34°41.440' N, 123°03.694' W), 4135 m depth, 30 October 2004, 1 fragment of shell (SIO M11435); (34°41.440' N, 123°03.694' W), 4135 m depth, 30 October 2004, 1 shell (SIO M11420); (34°41.015' N, 123°09.367' W), 4129 m depth, 26 February 2005, 1 specimen (SIO M11462); (34°41.920' N, 123°12.257' W), 4079 m depth, 21 June 2005, 1 fragment of shell (SIO M11488); (34°39.826' N, 123°5.241' W), 4070 m depth, 23 June 2005, 1 shell (SIO M11496). MEXICO. Off Bahía Magdalena, Baja California (24°23' N, 113°18.9' W), 3390–3580 m depth, 1 shell, leg. Lowenstam (CASIZ 156490). PERU, R/V USS ALBATROSS Expedition, station 4672, 88 mi (163 km) southwest of Palomino Light, 2845 fathoms (5200 m), shell with no body parts (HOLOTYPE, USNM 110563).

**Geographic Range:** This species, originally described from Peru, has also been found in Baja California, Mexico (Keen, 1971) and southern California (present paper).

**Remarks:** Our material of *Cyllichnium cylindrellum* from southern California clearly matches the original description and holotype of this species. The mid-whorl microsculpture shows the paired spiral grooves and the general outline of the shell is very similar to that of the holotype. Some variability has been observed in the southern California material, in some specimens the lip raises slightly above the apex (LACM 95-19.2, CASIZ

156490) (Figures 11, 13), whereas in others (LACM 95-126.3) (Figure 12) it does not.

Keen (1971) recorded this species from Bahía Magdalena, Baja California, Mexico. Keen's two illustrations are a copy of the original figure and the specimen from Bahía Magdalena (CASIZ 156490) on the right. Examination of the material confirmed that Keen's specimen also belongs to *C. cylindrellum*.

The reassignment of this species was here conducted based on anatomical features. The reproductive system of *C. cylindrellum* has the characteristic female copulatory organ found in other species of the genus (Bouchet, 1975; Valdés, 2008). Also, the radula is composed of a series of simple and hamate lateral teeth, very similar to those of the Atlantic species *C. waldae* and *C. africanum* (see Bouchet, 1975) as well as the Pacific species *C. ancillarioides*, *C. mucronatum*, and *C. nanum* (see Valdés, 2008).

*Cyllichnium cylindrellum* differs from other species of the genus by its shell morphology and internal anatomy. The shells of the Pacific species *C. ancillarioides* and *C. mucronatum* have much narrower bases and apertures, as well as more pointed apices (Valdés, 2008). The other Pacific species, *C. nanum* has a distinct columellar tooth (Valdés, 2008), absent in *C. cylindrellum*. Anatomically, *C. ancillarioides* and *C. mucronatum* have 10 and 6 radular lateral teeth, respectively (Valdés, 2008), whereas *C. cylindrellum* has 12. The reproductive system of *C. mucronatum* has a female copulatory organ with marginal papillae only, whereas in *C. cylindrellum* the entire organ is covered with papillae, as in *C. ancillarioides* (Valdés, 2008). However, the prostate of *C. ancillarioides* is much more elongated than that of *C. cylindrellum*, whereas the penis is shorter and wider.

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# Conservation of two endangered European freshwater mussels (Bivalvia: Unionidae): A three-year, semi-natural breeding experiment

Rafael Araujo

Museo Nacional de Ciencias Naturales-CSIC  
c/ José Gutiérrez Abascal 2  
28006 Madrid, SPAIN  
rafael@mncn.csic.es

Carles Feo

Quim Pou  
Miquel Campos  
Consorci de l'Estany  
Plaça dels Estudis 2  
17820 Banyoles, Girona, SPAIN  
cfeo@consorciodelestany.org  
qpou@consorciodelestany.org  
mcampose@consorciodelestany.org

## ABSTRACT

Freshwater mussels are among the most imperilled of all animal groups. The populations of the endangered *Unio mancus* Lamarek, 1819 and *U. ravaoisieri* Deshayes, 1847 (both designated as *U. elongatulus* C. Pfeiffer, 1825 in the European Habitat Directive) have declined severely over recent years in Spain. To conserve these species in Lake Banyoles (Girona, Spain), a total of 108,875 *U. mancus* and 27,423 *U. ravaoisieri* juveniles produced by artificial infection of larvae on host fish were grown in a number of semi-natural, sequential breeding systems, which involved the use of water and sediment from their natural habitat, plus pools, plastic outdoor channels, and/or cages. Across the tested systems, *U. mancus* reached a mean length of 9.7 mm ( $SD \pm 1.53$ ) in one year and 12.4 mm ( $SD \pm 1.55$ ) in two years; for *U. ravaoisieri* these values were 15.8 ( $SD \pm 0.76$ ) and 21.2 mm ( $SD \pm 2.45$ ). In a experiment adding extra food, the growth rates were much lower than those recorded for the other systems. In October 2013, 278 2+ juveniles of *U. mancus* and 224 2+ juveniles *U. ravaoisieri* were released into the lake, increasing their original populations by some 40% and 200% respectively. Preliminary observations made eight months later showed that several tens of these mussels were still alive. The large numbers of juveniles raised in the semi-natural systems will help conserve future generations for these bivalves in Lake Banyoles. Over the three years of the project, 3,510 fish infected with a total of some 500,000 glochidia of one or the other species were also released. After 1.5 years, hundreds of juveniles (13–35 mm) arising from this release were detected. This is the first time in Europe that thousands of juveniles of any endangered freshwater mussel species have been bred in captivity without the addition of extra nutrients, demonstrating the practicality of low-tech and economical approaches to mussel population restoration.

*Additional Keywords:* *Unio*, *Unio elongatulus*, *Unio mancus*, *Unio ravaoisieri*, growth, juveniles, restocking, Lake Banyoles

## INTRODUCTION

Freshwater mussels, or naiads (Order Unionida), are among the most imperilled of all animal groups. Their numbers have drastically declined due to pollution, habitat deterioration, and declining numbers of host fish (Lydeard et al., 2004; Strayer et al., 2004). More than half of the USA's near 300 species are now either extinct, endangered, or threatened, and in Europe the extinction rate for naiad populations is growing (Cuttelod et al., 2011). In the USA, this scenario has encouraged attempts to develop naiad captive breeding techniques—work that has inspired similar attempts in Europe. The first documented studies on naiad artificial reproduction and propagation were performed on commercial species in the USA (Lefevre and Curtis, 1912; Coker et al., 1921; Howard, 1922); nacre for buttons was of great economic importance in North America at the beginning of the 20th century (Anonymous, 1914; Claassen, 1994). In addition to providing an excellent compendium of the natural history of freshwater mussels, these pioneering papers summarized knowledge on mussel breeding and cultivation that is still useful today.

The reproductive strategy of freshwater mussels involves an obligatory parasitic stage, in which the larvae (glochidia) attach to the external surface of a suitable host and metamorphose into free-living juveniles (Lefevre and Curtis, 1912; Kat 1984; Wachtler et al., 2001; Araujo et al., 2002; Rogers-Lowery and Dimock Jr, 2006; Barnhart et al., 2008). This, of course, is a major problem in the development of controlled naiad breeding systems. Controlled breeding, of which the main objective is to obtain larger numbers of juveniles from fish infected with glochidia than would be naturally produced, can be carried out in captivity or semi-captivity. Juveniles then need to be grown before their introduction

into natural habitats where populations have been depleted or entirely lost.

Gum, Lange, and Geist (2011) recently published a critical reflection on some of the captive breeding techniques used in Europe and the USA, with emphasis on those for the freshwater pearl mussel *Margaritifera margaritifera* (Linnaeus, 1758). The information in the latter work, and in other seminal publications in the field (see below) was used to develop the successful semi-natural systems for rearing endangered freshwater mussels reported here.

Along with the process of fish infection, the provision of an adequate diet for juveniles is a key problem that must be solved. The success of Lefevre and Curtis (1912), Coker et al. (1921), and Howard (1922) in rearing juveniles of several species was dependent on the use of the water, food, and sediment present in the mussels' natural ecosystems. The idea that these elements were necessary was confirmed many years later in Europe by Hruska (1999), who hypothesized that the food required by *M. margaritifera* juveniles comes from a healthy rhizosphere. Eutrophication, contamination, and silting of the immediate environment was deemed responsible for the absence of available habitat, juvenile food and the recruitment of young mussels. The success of Hruska (1999), who grew juveniles larger than 5 cm, relied on river bank restoration and a semi-captive breeding system that provided for natural feeding. In Spain, Comas and Valls (2007) grew juvenile *Unio mancus* Lamarek, 1819 to reproductive age in a system involving minimum management that made use of natural water and sediment—but not from the river were the mussels normally lived—without any extra nutrients. However, this work was only published as an internal document of the Catalan Regional Government. Other authors have developed more controlled systems (with more or less success) inspired by systems used in marine bivalve aquaculture, providing extra food in the form of algae (Hudson and Isom, 1984; Gatenby et al., 1996; Gatenby et al., 1997; O'Beirn et al., 1998; Henley et al., 2001; Araujo et al., 2003; Gatenby et al., 2003; Beck and Neves, 2003; Liberty, 2004; Guyot, 2005; Jones et al., 2005; Barnhart, 2006; Kovitvadhi et al., 2006; Liberty et al., 2007; Eversole, 2008; Kovitvadhi et al., 2008). These more controlled systems have inspired the main cultivation programs for *M. margaritifera* in Europe (Gum et al., 2011; Eybe, et al., 2013).

Although the use of algae has sometimes been successful in the rearing of presumably healthy juveniles, Nichols and Garling (2000, 2002) report the main dietary source of carbon for naiads living in rivers and lakes to be bacterial. Algae do, however, appear to provide key nutrients such as vitamins and phytosterols. Much remains to be learned about the diet of juvenile naiads in natural environments and in captivity. As part of the LIFE 08 NAT/E/000078 "Estany Project" which is dedicated to restoring the native aquatic fauna of Lake Banyoles (Girona, Spain; a Natura 2000 site), semi-natural systems were developed to rear two endangered European species of mussel: *U. mancus* and *U. ravoisieri* Deshayes, 1847

(both designated as *U. elongatulus* C. Pfeiffer, 1825 under the Habitat Directive, the main European law for species conservation). The first of these species lives in Spanish and French Mediterranean rivers; the limit of its eastward range, however, remains unknown (Araujo et al., 2009a; Prié and Puillandre, 2013). It is considered "near threatened" by the IUCN (Cuttelod et al., 2011). The second species, *U. ravoisieri*, is restricted to just two localities in Spain (Araujo et al., 2009a; Khaloufi et al., 2011). The Lake Banyoles populations of both species have been in severe decline in recent years, a consequence of the proliferation of invasive predatory fish. The five native fish species (*Anguilla anguilla*, *Gasterosteus aculeatus*, *Barbus meridionalis*, *Squalius laietanus* and *Salaria fluviatilis*) have been partially eliminated and replaced by the exotic *Micropterus salmoides*, *Lepomis gibbosus*, *Cyprinus carpio*, *Perca fluviatilis*, and *Sander luciperca* (Moreno-Amich et al., 2006).

It was hypothesized that cultivation systems connected to the natural habitat of these naiads would provide the unknown natural food required by the juveniles. This paper presents the first large-scale attempt to raise juveniles of endangered naiad species in Europe, using water and sediment from the mussels' natural environment.

## MATERIALS AND METHODS

The work was performed at the Naiad Breeding Laboratory at Banyoles (Girona, Spain). This field station is located 500 m from Lake Banyoles (which lies in the Ter Basin) and receives a constant supply of lake water. Although in preliminary work several fish species were tested (including *Salaria fluviatilis*, *Luciobarbus graellsii*, *Phoxinus phoxinus*, and *Tinca tinca*) as hosts for the mussel larvae, *Barbus meridionalis* Risso, 1827 and *Squalius laietanus* Doadrio, Kottelat and Sostoa, 2007 were chosen since these species are native to the lake. The two naiad species raised were *U. mancus* and *U. ravoisieri*, both of which are native to the lake basin. The number of specimens of fish and naiads involved differed over the three years of the project (2010–2013) (Table 1).

The fish used as hosts were collected from the Rivers Ter, Terri, Brugent, Llémena and Osor (all in the Ter Basin), 1–4 weeks before infection with glochidia. Following capture these fish were maintained in outdoor pools (1,600 L) that received a flow of lake water.

The gravid naiads used came from the lake (*U. ravoisieri*) or its effluents (*U. mancus*); these were collected over the spring (the water temperature of the lake was monitored six times per day using a submerged thermometer (Thermotronic Getech Innova) to determine the water temperature suitable for the reproductive cycle to begin). These mussels were maintained in indoor aquaria for the collection of released glochidia (these remained viable for 48–72 h); they were then returned to their natural habitat. Mature glochidia were collected with pipettes and placed in aerated water for 5 min in a plastic Tupperware vessel (500 ml) containing a single fish. Infected fish were then

**Table 1.** Fish and naiad specimens used.

Barbus meridionalis	TOTAL	<i>U. mancus</i>			<i>U. ravoisi</i> eri				
		2011	2012	2013	Total	2011	2012	2013	Total
Infected	3412	188	705	1038	1931	51	232	1198	1481
Released to the lake	2507		436	839	1275		150	1082	1232
Infected at the lab	905	188	269	199	656	51	82	116	249
Survivors at the lab	637	67	255	174	496	18	56	67	141
% survivors	70.3	35.6	94.8	87.4	75.6	35.3	68.2	58	56.6
<i>Squalius laietanus</i>									
Infected	1236	62	973	73	1108	46	18	64	128
Released to the lake	1003		871	73	944		0	59	59
Infected at the lab	233	62	102	0	164	46	18	5	69
Survivors at the lab	100	29	37	0	66	20	9	5	34
% survivors	42.9	46.8	36.6	100	40.2	43.5	50	100	49.2

kept in aerated conical tanks (180 L) at a temperature ranging between 15 and 22 °C; only fish infected over the same 3-day period were placed in the same tank. These tanks were equipped with biological and mechanical filters. The fish were provided feed every day until three days before the release of juveniles. The number of degree-days needed for metamorphosis to occur was based on Araujo et al. (2005) and Reis et al. (2013). The water in these tanks was filtered (filter mesh size 200 µm) and renewed three times per day.

Two days before juvenile release, a 200 µm mesh collector was installed in the water circuit to retrieve them. This collector was checked and juveniles collected once or twice daily until no more were found.

The juveniles obtained were observed under a binocular microscope to check their viability; those deemed alive were then assigned to either (Figure 1):

System 1) Plastic tray (240 cm long, 60 cm wide, 17 cm high) containing 5 cm-deep un-sieved lake sediment (water depth to sediment surface = 9 cm) supplied with a constant water flow. This system was maintained indoors under

normal photoperiod conditions. Juveniles of both naiad species were placed together in this system. Survival was checked periodically and a random sample of specimens measured until the emptying of the system in October 2013, or:

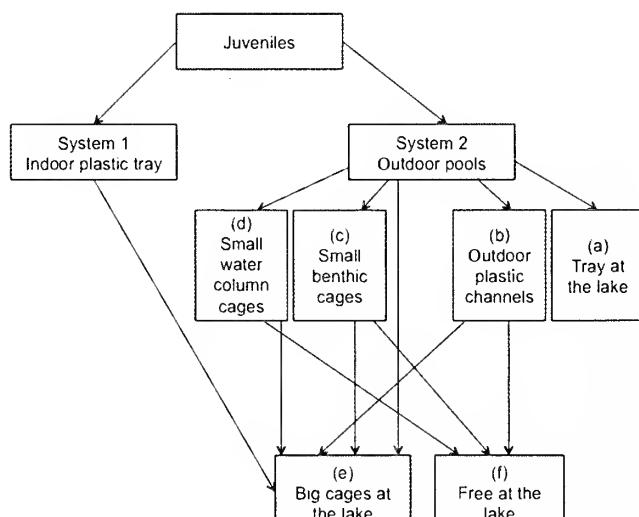
System 2) Three outdoor cubic pools (150 × 150 × 150 cm) containing 20 cm-deep un-sieved lake sediment, (water depth to sediment surface = 110 cm) supplied with a constant water flow. *Unio mancus* juveniles were released into pool 1 and *U. ravoisi*eri into pool 2 in 2011 and 2012; in 2012 the two species were also released together in pool 3. Survival was checked periodically and a random sample of specimens measured until pools 1 and 2 were emptied and the sediment filtered in February 2013, and until the same was performed with pool 3 in October 2013. [Note: new generations of *U. mancus* and *U. ravoisi*eri are currently being raised in pools 1 and 2].

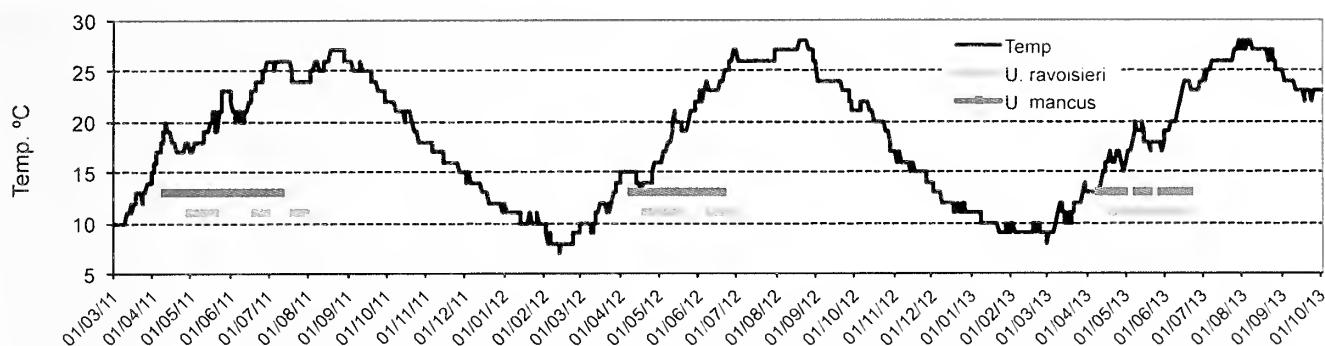
The surviving juveniles from System 2 were seeded into the following subsystems in February, April and October 2013 (Figure 1):

- plastic tray containing lake sediment (depth 30 cm), placed at the bottom of the lake (depth 2 m).
- outdoor plastic channels (6 m long, 50 cm wide, 28 cm high) containing 10 cm-deep lake sediment, supplied with a 1 L/s constant water flow (water velocity 50–100 cm/min) from the lake. Survival was checked periodically and a random sample of specimens measured each time until the end of the project.
- plastic cages (30 × 15 × 15 cm; mesh 1 × 1 cm) placed on the lake bottom (depth 2 m) (only *U. mancus*).
- cages (30 × 15 × 15 cm; mesh 1 × 1 cm) placed in the lake water column (depth 1 m) (only *U. mancus*).
- cages (100 × 25 × 25 cm; mesh 1 × 1 cm) placed on the lake bottom (depth 2 m).
- directly on the bottom of the lake in areas with no vegetation (only specimens produced in 2011 that reached a size of at least 2.5 cm).

Although the aim of the present work was to demonstrate the effectiveness of the natural diet (food from water and sediment) in raising the mussels, an experiment involving an external food source was also designed.

In 2012, 2000 *U. mancus* juveniles were divided into 5 series of 200 (two replicas) in Tupperware vessels

**Figure 1.** Schematic diagram of the experimental design.



**Figure 2.** Lake temperature and glochidial release season for *Unio mancus* and *U. ravoisiéri* over the three years of the experiment.

containing the following: 1) 400 ml lake water; 2) 400 ml lake water plus 0.8 ml of dehydrated commercial algae ( $66.5 \times 10^9$  cells of *Nannochloropsis*,  $11.08 \times 10^9$  of *Phaeodactylum* and  $1.25 \times 10^9$  of *Tetraselmis*); 3) 400 ml lake water plus a mixture of 2.4 ml of natural algae, leafs and macrophyte extract; 4) 400 ml lake water plus 0.8 ml of leaf extract and 0.8 ml of dehydrated commercial algae; and 5) 400 ml lake water plus 0.8 ml of biofilm extract.

Leaf extract was obtained by washing macrophytes and the leafs and stems of land plants from the habitat around the lake; the suspension obtained was filtered and frozen in doses of 0.8 ml. Biofilm extract was prepared from 200 g of the biofilm growing on the walls of the outdoor pools in 2 l of lake water; this was also filtered and frozen in doses of 0.8 ml.

All containers were cleaned once per week; dead juveniles were removed, live juveniles were measured, and the food renewed. The experiment ran between May 2012 and July 2013. The surviving juveniles were transferred into the lake in their own cage.

We performed a one-way ANOVA to compare the growth among some of the different systems.

## RESULTS

In 2011–2013, the release of glochidia by *U. mancus* and *U. ravoisiéri* occurred between April 11 and July 22, and April 27 and July 24, respectively (minimum lake temper-

ature 13°C) (Figure 2). The total number of *U. mancus* and *U. ravoisiéri* juveniles released by the host fish for use in the different systems was 108,875 and 27,423 respectively (Table 2). The release of juveniles from the host fish occurred between days 7 and 33 post infection (PI) in *U. mancus* and 8 and 26 PI in *U. ravoisiéri*, depending on the water temperature (representing a minimum 145 and maximum 521 degree-days for both species taken together) (Table 3).

All the systems used in this study successfully raised mussels, but with marked differences in survival and growth rates. All the juveniles in the indoor plastic tray (System 1) in 2011 died due to a hardware malfunction, but in 2012 System 1 was capable of maintaining live juveniles (Figure 3). Those that survived one year (12%) reached a mean length of 4.5 mm ( $SD \pm 1.35$ ,  $n=102$ ) and a maximum of 8 mm. The total survival rate at day 520 was 3.6%, with 574 live juveniles recovered (mean size 6.5 mm, minimum 3.5 mm, and maximum 11.5 mm) for the 16,322 originally seeded.

The best results were obtained with the outdoor pools (System 2). In 2011, 3,000 *U. mancus* juveniles were placed in pool 1 and about 1,800 *U. ravoisiéri* in pool 2. In 2012 these figures were 9,380 *U. mancus* and 5,005 *U. ravoisiéri* in pools 1 and 2 respectively. In addition, 16,658 *U. mancus* and 2,412 *U. ravoisiéri* were mixed in pool 3. [Note: in 2013, once the juveniles from pools 1 and 2 had been removed and the pools cleaned, 36,140 *U. mancus* and 4,318 *U. ravoisiéri* were placed in them respectively].

**Table 2.** Number of juveniles obtained from host fish, and numbers seeded in the different systems. Uma = *Unio mancus*. Ura = *U. ravoisiéri*.

	2011		2012		2013		Total	
	Uma	Ura	Uma	Ura	Uma	Ura	Uma	Ura
Aquaria	329		489				818	0
Indoor plastic tray	7464	1592	15 447	875			22 911	2467
Outdoor pools	~3000	~1800	28 831	9719	36 140	4318	67 971	15 837
Outdoor channels					7766	9119	7766	9119
Tupper			2653		601		3254	0
Lake			517				517	0
Lake streams and channels			5638				5638	0
<b>TOTAL</b>	<b>10 793</b>	<b>3392</b>	<b>53 575</b>	<b>10 594</b>	<b>44 507</b>	<b>13 437</b>	<b>108 875</b>	<b>27 423</b>

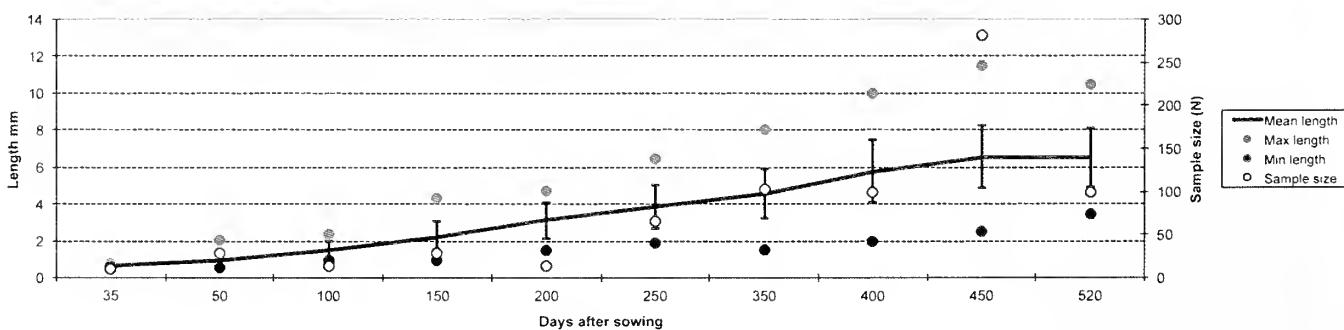
**Table 3.** Number of juveniles of *Unio ravoisi* (above) and *U. mancus* (below) obtained per infection, fish species and year. B = *Barbus meridionalis*, S = *Squalius laetanus*.

	Month	Year	Fish	N fish	N juveniles	Temp	Days (max)	Degree/days (max)
<i>U. ravoisi</i>	May	2011	S	5	1230	17.3	15–24 (19)	260–400 (330)
	April	2012	B	3	85	18.2	16–26 (22)	300–470 (400)
	May		B	7	5068	18.4	13–21 (19)	230–390 (350)
	July		B	6	278	21.4	11–17 (12)	235–365 (260)
	July		S	13	1216	21.4	11–17 (12)	235–365 (260)
	May	2013	B	18	2435	17.3	11–24 (19)	195–400 (330)
	May		B	30	3431	19.8	13–23 (15)	250–460 (290)
	June		S	8	336	22.0	8–15 (11)	175–325 (240)
	June		B	21	1677	22.6	8–15 (10)	175–340 (230)
	June		B	4	177	20.8	9–14 (12)	185–290 (250)
<i>U. mancus</i>	April	2011	B	7	838	17.0	17–23 (21)	285–390 (355)
	April		S	7	1279	17.1	17–26 (21)	290–445 (360)
	July		S	10	1774	20.9	10–17 (12)	215–355 (260)
	July		B	29	3610	21.0	10–17 (12)	210–360 (250)
	April	2012	S	18	5712	16.6	19–28 (21)	275–450 (325)
	April		S	9	294	15.1	19–26 (25)	280–390 (375)
	April		B	57	4075	16.3	18–33 (26)	232–521 (379)
	April		B	10	728	18.1	17–24 (19)	290–420 (325)
	May		B	82	35 356	18.8	12–25 (17)	190–465 (300)
	May		B	35	1156	19.2	14–22 (16)	260–425 (300)
	June		B	13	2551	21.5	10–19 (13)	200–400 (275)
	June		B	19	2731	21.5	7–19 (11)	145–410 (235)
	June		S	4	271	22.1	9–19 (13)	190–400 (275)
	April	2013	B	90	16 082	16.4	18–28 (23)	275–460 (364)
	April		B	10	2539	16.7	17–26 (21)	260–430 (335)
	April		B	54	21 987	16.8	17–25 (23)	345–437 (375)
	June		B	20	3825	21.0	9–17 (13)	190–360 (270)

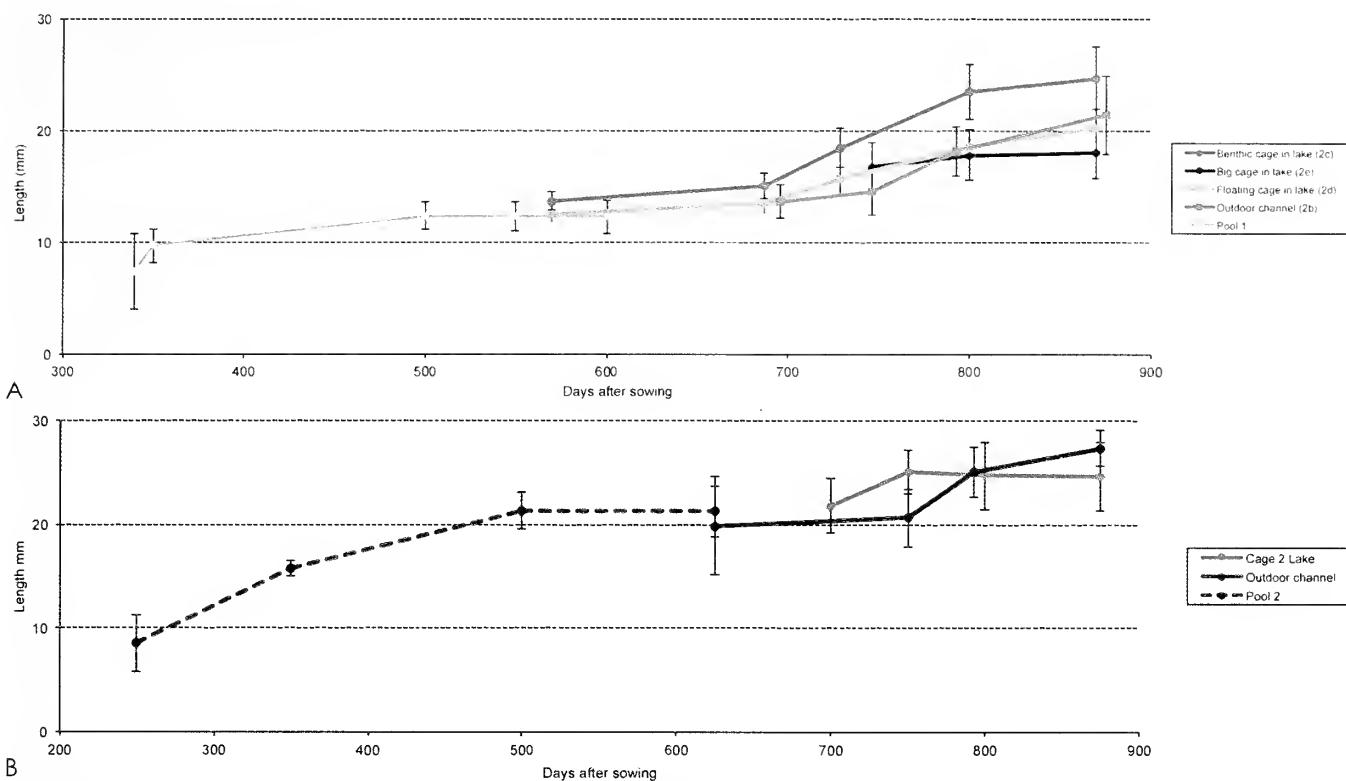
Between summer and autumn 2012 there was a serious loss of juveniles in pool 1 probably due to the overgrowth of benthic algae; this problem was solved by cleaning the floor of the pool and covering the top. On day 350, 100 juveniles ( $\geq 1$  cm) from pool 1 were transferred to a tray in the lake (System 2 a), and on day 575, 150 (1–1.5 cm) were transferred to the small cages described for System 2 c and d. On day 617, the pool was siphoned and a large number of empty shells detected. A total 493 remaining live juveniles were placed either in the outdoor plastic channels (System 2 b) or a large cage on the lake bottom (System 2e) (Figure 4A). On day 697, 100 juveniles (2–2.5 cm) from pool 2 were transferred to

a large cage in the lake (System 2 e), and the remaining 237 distributed between the outdoor plastic channels (System 2 b) and a large cage in the lake (System 2 e) (Figure 4B). On day 325, 129 juveniles were transferred from pool 3 to a large cage in the lake (System 2 e). On day 500, the pool was siphoned and the 1,459 remaining juveniles detected transferred to another large cage in the lake (System 2 e).

The estimated survival rate at 1 year for the 2011 generation of *U. mancus* in pool 1 before any distribution into any subsystem was 77%. However, this fell to 20% after two years. The juveniles reached a mean length of 9.7 mm ( $SD \pm 1.53$ ,  $n=220$  measured) after one year, and 12.4 mm



**Figure 3.** Growth of the juveniles seeded in 2012 in the indoor plastic tray (System 1) (both naiad species mixed). N indicates the number of measured juveniles.



**Figure 4.** Juvenile growth in the different systems. A. *Unio mancus*. B. *U. ravoisiere*.

( $SD \pm 1.55$ ,  $n=191$  measured) after two (Figure 4A). The generation of juveniles seeded in 2012 were killed by the algal growth on the bottom.

In pool 2, the survival rate of the *U. ravoisiere* 2011 generation was 33% for the first year, and 18% for the second. The mean length reached at the end of the first and second years was 15.8 mm ( $SD \pm 0.76$ ,  $n=22$  measured) and 21.2 mm ( $SD \pm 2.45$ ,  $n=331$  measured) respectively (Figure 4B). The survival rate of the 2012 generation was 0.7%.

On day 500, the survival rate of the mixed population in pool 3 was 8.2% and the mean length 11 mm ( $SD \pm 2.95$ ,  $n=300$  measured).

The survival and growth rates strongly increased when juveniles reached two years (2+) of age and a size of 1–1.5 cm in *U. mancus* (Figure 4A) and 2–2.5 cm in *U. ravoisiere* (Figure 4B). Of the 493 *U. mancus* 2+ juveniles in pool 1, 200 were transferred to a cage in the lake (System 2 e) and the rest to an outdoor plastic channel (System 2 b). After 170 days, the survival rates were 100% in the plastic channel and 93% in the cage, and the corresponding mean lengths were 2.1 ( $SD \pm 2.33$ ) and 1.8 cm ( $SD \pm 2.3$ ). In a similar experiment with *U. ravoisiere* 2+, the same survival rates were recorded but the mean lengths were much greater: 2.5 cm ( $SD \pm 3.31$ ) and 2.7 cm ( $SD \pm 2.3$ ) respectively. In October 2013 (i.e., at 870 days of age) a small portion of the juveniles in the outdoor plastic channels were maintained there; the rest were placed in the lake, both in cages (System 2 e) and free (System 2 f). In May 2012, prior to the use of the cages in

the lake, 100 *U. mancus* juveniles of 1 cm from pool 1 were put in an open tray with sediment and placed in the lake (System 2 a). After three months the tray was removed; no living specimens were found but only broken shells, suggesting that they had fallen prey to fish and crayfish. However, in October 2012, upon inspection of the mud underneath where the cage had lain, a mussel was found measuring 28.1 mm (this mussel was marked for identification purposes), and in June 2013, another was found measuring 38 mm. This means that the first juvenile grew 17 mm in the five months since the cage was placed in the lake (May 2012) and the second 28 mm in 13 months. However, this subsystem was no longer used given the poor results obtained.

The survival rate at 295 days for the 150 *U. mancus* juveniles from pool 1 in the small cages in the water column and at the bottom of the lake (Systems 2 c and d), was very high at 83% and 86%, respectively. Growth, however, was greater in the cage on the bottom (System 2 c) ( $F=93.7$ ,  $p<0.001$ ) (Figures 4A, B). Indeed, the specimens in the water column cages were covered in algae and some showed deformities. The large, bottom-placed cages (System 2 e), though successful (Figures 4A, B) were difficult to handle. All the cages became covered in calcified algae during spring and summer, blocking the mesh and thus reducing oxygen and water flow. In October 2013, all the juveniles from all these cages were removed, labeled and placed once more in the lake, either in large cages (System 2 e) or free (System 2 f).

Over the three years of the project, 3,510 infected fish carrying an estimated total 500,000 *U. mancus* and *U. ravaoisieri* glochidia were released into the lake and its effluents (Table 1). In May and July 2013 hundreds of 1.5 year-old (13–35 mm) juvenile mussels were observed in these outflows.

The results suggest that *U. mancus* reaches 9.7 mm by the end of its first year and 12.5 mm at the end of the second (taking all System 2 subsystems together and excluding System 1). For *U. ravaoisieri*, these values are 15.8 and 21.2 mm. However, the growth rate is not constant over the year; growth stops between November and March (Figures 4A, B).

In the experiments involving the provision of extra food, one replica was followed for 400 days and the other 350. Although growth rates were reduced (maximum 2 mm in one year when provided with commercial algae and leafs; Figure 5) compared to the above tested systems, all survivors were placed in a large cage on the bottom of the lake (System 2e) in October 2013. At 350 days from the beginning of the experiment, only two of the five series had juveniles alive, both in the two replicas, the one with algae and the other with algae and leaf extract. The growth between the replicas didn't have significant differences ( $p>0.02$ ), but it was different between the two series. The juveniles fed algae and leaf extract grew more than the others ( $F=35.61$ ,  $p>0.001$ ). However, the growth rates of the *U. mancus* juveniles of the experiment were less than the ones of the pool 1-system 2 ( $F=1575.6$ ,  $p>0.001$ ) or the plastic tray-system 1 ( $F=271.9$ ,  $p>0.001$ ).

In summary, the numbers of live juveniles (Figure 6) raised were: *U. mancus*: 218 2+ and 43,700 0+; *U. ravaoisieri*: 100 2+, 64 1+ and 13,400 0+, plus a mixture (unknown proportions) of 2,304 1+ *U. mancus* and *U. ravaoisieri* raised in pool 3.

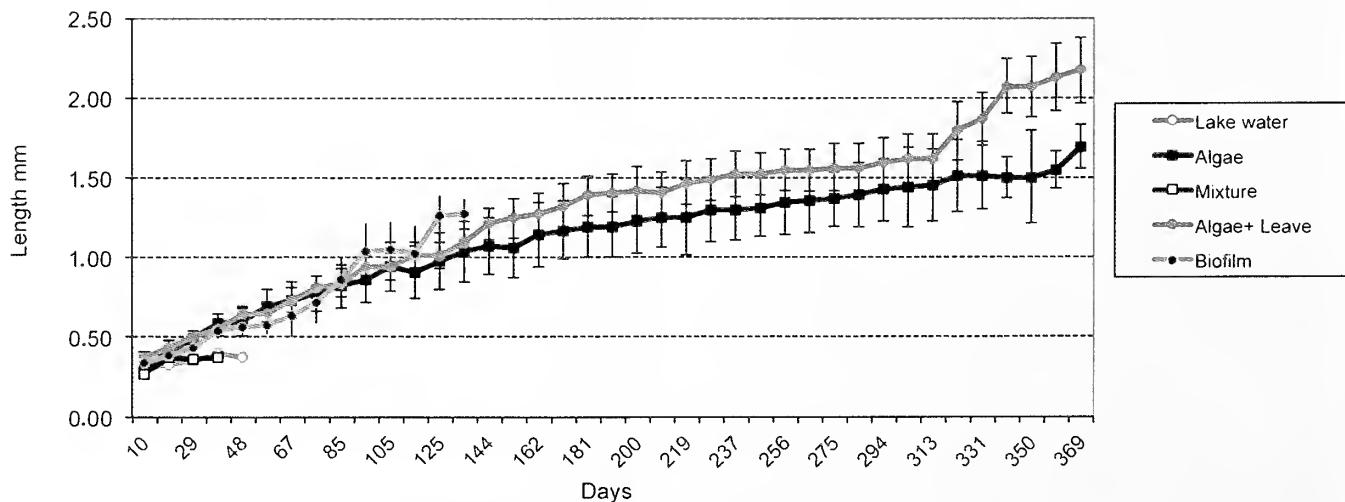
A total of 278 and 224 2+ juveniles of *U. mancus* and *U. ravaoisieri*, were released free into the lake, representing improvements of 40% (estimated population

$1,000\pm500$ ) and 200% (estimated population  $110\pm50$ ) of their original populations (M. Campos, pers. observ.).

## DISCUSSION

Seminatural breeding efforts to rescue endangered pearl mussel populations can result in adverse effects such as genetic drift and selection (Geist, 2010), so they should only be considered as an emergency measure. The goal of this work was to obtain large numbers of juveniles of two endangered freshwater mussels, *U. mancus* and *U. ravaoisieri*, raising them in a system involving water and sediment from their natural environment. The sequential systems tested maintained juveniles in pools or plastic channels at a field station, before releasing them into the wild. The large numbers of 1–3 years old juveniles maintained at the field station and in the lake offers hope for these endangered species. This is the first time in Europe that thousands of juveniles of any endangered freshwater mussel have been bred in captivity for three years without the addition of extra nutrients.

Although thousands of viable juveniles were raised, mortality was high, especially during the first year of life. The mortality recorded in the pools in 2012 was probably caused by algal overgrowth and subsequent anoxia. This can be avoided by covering the pool and/or siphoning and filtering the upper layer of the sediment, and renewing it after two years. The use of outdoor plastic channels with a slow water current—but fast enough to prevent deposition—can also be used. Although no natural mortality data are available for these species, juvenile mortality is commonly high among freshwater mussels (Young and Williams, 1984). The juveniles that reached two years seemed to show increased viability. The raising of mussels for one or two years in pools and then transferring the survivors to outdoor channels or bottom-lying cages in the wild, would likely provide very good results (Figures 4A, B).



**Figure 5.** Survival and mean growth of the juveniles fed with extra food. Results are means for the two replicas.



**Figure 6.** The juveniles bred. A. Empty shells of *Unio mancus* and B. *U. ravoisi* 2+ from System 2e. Scale bar: 1 cm. C. Live juveniles labeled for release into the lake.

The main problem encountered with the use of the cages (of both sizes) was the growth of calcified algae (probably a consequence of the hard water of Lake Banyoles); this blocked the mesh and isolated the mussels from the environment. This could be avoided by regular cage cleaning. This blocking was probably the reason why the *U. ravoisi* juveniles grew better in the outdoor plastic channels (System 2b) than in the cages (System 2e) (Figure 4B) ( $F=93.7$ ,  $p<0.001$ ). At 2 or 3 years of age, the mussels raised in cages are mature enough to be released into the wild.

The survival of the juveniles freely seeded in the lake (System 2f) remains to be fully studied, but preliminary observations (June 2014) suggest that they are still alive. The release of infected fish was also shown to be a successful way of seeding the environment, at least in the lake effluents. This could be an easy and effective means of repopulating depleted areas but it would also be very difficult to monitor, and success might vary between one water system and another.

The results obtained with the indoor plastic trays (System 1) were not as good as those obtained with the pools (System 2 and its subsystems); survival and growth were much slower (Figure 3) ( $F=66.89$ ,  $p<0.001$ ). However, these trays provide an easy way of maintaining juveniles for study and handling in the laboratory.

In the experiment in which extra food was added (which was very laborious), the growth rates were much lower than those recorded for the other systems, although some juveniles did survive for more than one year (Figure 5).

The fish populations of Lake Banyoles have completely changed over the last century. The five native fish species (*Anguilla anguilla*, *Gasterosteus aculeatus*, *Barbus meridionalis*, *Squalius laietanus*, and *Salaria fluviatilis*) have been partially eliminated and replaced by the exotic *Micropterus salmoides*, *Lepomis gibbosus*, *Cyprinus carpio*, *Perca fluviatilis* and *Sander luciperca* (Moreno-Amich et al., 2006). This led to the vanishing of the formerly abundant populations of *U. mancus* and *U. ravoisi*.

Restocking with native fish and naiads using the present systems is vital for the survival of these endangered molluscs in the lake.

In recent years, our knowledge of the reproductive biology of several *Unio* species has greatly increased (Aldridge and McIvor, 2003; Araujo et al., 2005; Vincentini, Araujo et al., 2009b; Reis et al., 2013); this information could be used to better conserve these endangered freshwater mussels. The present results increase our knowledge of the reproductive strategy of *U. mancus* and *U. ravoisi*. Several species of fish have been reported as successful hosts for the production of *U. mancus*

juveniles (Araujo et al., 2005), to which *B. meridionalis* and *T. tinca* (results not shown) can now be added. In *U. ravoisi*, the breeding season of which was unknown, we now have shown that glochidia are released between April and July, and *B. meridionalis*, *S. laetanus*, *L. graelsi*, *S. fluviatilis*, *T. tinca* and *P. phoxinus* may be valid hosts, as shown in this work and preliminary testing.

Although much remains to be learned regarding the diet of freshwater mussels, the present results show that some species can be cultured in semi-captivity using only the water and sediment from their natural ecosystem. The survival rate of these juveniles in the following years will give a better idea about the viability of these breeding systems.

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# A new species of *Glyphostoma* (Gastropoda: Clathurellidae) from the Gulf of Mexico

Emilio F. Garcia

115 Oakcrest Dr.  
Lafayette, LA 70503 USA  
Efg2112@louisiana.edu

## ABSTRACT

*Glyphostoma coronaseminale* new species is described and compared with the Western Atlantic species *G. dentiferum* Gabb, 1882, *G. epicasta* Bartsch, 1934, *G. gabbii* (Dall, 1889), *G. golfoyaquense* Maury, 1917, and *G. herninea* Bartsch, 1934.

## INTRODUCTION

Two decades of research campaigns conducted in the Gulf of Mexico by the Biology Department at the University of Louisiana at Lafayette (ULL) have led to many molluscan discoveries (e.g., Garcia, 2003, 2005, 2006). The cruises have utilized the R/V PELICAN, a ship managed by the Louisiana Universities Marine Consortium (LUMCON).

In September, 2014 a cruise that terminated west of Dry Tortugas, Florida, was conducted by ULL marine biologists Drs. Darryl Felder and Suzanne Fredericq. This was the last of five cruises executed under the designation Gulf of Mexico Research Initiative (GoMRI). Two types of dredges were used, the standard box dredge and the Benthic Skimmer, a large, more efficient dredge specially designed for soft bottom (see García, 2007a). This dredge was in use when the holotype of the *Glyphostoma* species described herein was collected.

The genus *Glyphostoma* was erected by Gabb for the fossil taxon *G. dentiferum*; it is known from the Pliocene and Miocene of the Caribbean and the southeastern United States, but it is also part of the recent fauna. Powell (1966: 115) considered this taxon to be mostly American. Although it had been used for recent Indo-Pacific species, most of these could be assigned to either *Etrema* or *Lienardia*. Nevertheless, many Recent Indo-Pacific species have been assigned to *Glyphostoma* (WoRMS, 2014).

In the Western Atlantic, the genus *Glyphostoma* can only be confused with *Lioglyphostoma* Woodring, 1928, which differs by the lack of labral denticles and the “growth wrinkles on the anal fasciole” (Woodring, 1928:

193). These “wrinkles”, characteristic of the *Glyphostoma* species described so far, are lacking in the species described here; they have been substituted by well-defined nodes, therefore differentiating the sculpture of the anal fasciole from all other Western Atlantic *Glyphostoma*.

## SYSTEMATICS

Family Clathurellidae H. Adams & A. Adams, 1858

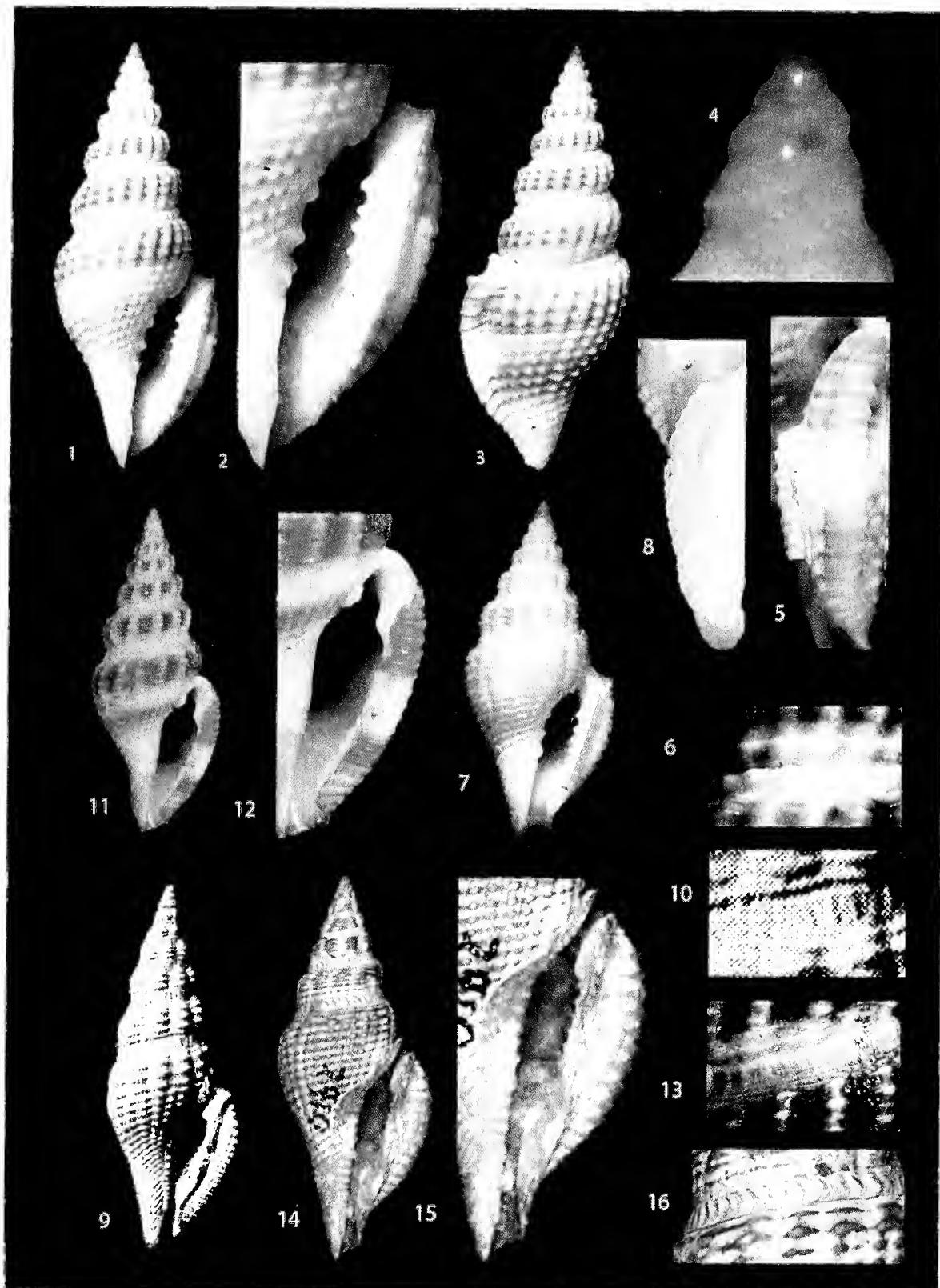
### Genus *Glyphostoma* Gabb, 1872

**Type Species:** *Glyphostoma dentiferum* Gabb, 1872, by monotypy.

#### *Glyphostoma coronaseminale* new species (Figures 1–8)

**Diagnosis:** A white shell with a wide peripheral pale-yellow band on apical whorls and a second, anteriorly positioned band of the same color on last whorl; with a constricted anal fasciole ornamented with spirally extended nodes, and a parietal wall showing a nodose callus at entrance of anal fasciole, a posterior denticle, two centrally positioned plicae, and an anterior denticle followed by increasingly smaller, at times very weak, nodules.

**Description:** Holotype (Figures 1–6) 23.2 mm in length, strong, fusiform (length/ width ratio 2.64). Protoconch (Figure 4) conical, of approximately 3.25 smooth, yellowish whorls; first whorl minute, translucent; following whorls developing a sub-medial keel of increasing strength; a second, short keel appearing anteriorly, just above suture, towards termination of last whorl. Transition to teleoconch indicated by a shallow, strongly sinuous scar, a change in coloration from yellowish to white, and the beginnings of the adult sculpture. Teleoconch of 7.5 convex, subsuturally constricted whorls, creating a shoulder. Suture strongly impressed on early whorls, narrowly channeled on later whorls, crenulated by a row of strong nodes on anal fasciole (Figure 6). Axial sculpture of strong opisthocone, rounded ribs of even size, as wide as interspaces; 10 ribs on first whorl, progressively increasing to 24 on last whorl, almost reaching anterior end before evanescing; last two



**Figures 1–16.** *Glyphostoma* species. 1–8. *Glyphostoma coronaseminale* new species. 1–6. Holotype USNM 1274997, west of Dry Tortugas, SW Florida: 25°31.091' N, 84°28.391' W to 25°27.939' N, 84°27.145' W; in 352–361 m, 23.2 mm. 7–8. Paratype USNM 1274998, southwest of Key West, Florida, in 84 m, 17.2 mm. 9–10. *Glyphostoma golfoyaquense* Maury, 1917, type figure (after Maury), Rio Cana, Santo Domingo, 20 mm. 11–13. *Glyphostoma gabbii* (Dall, 1889). Syntype, USNM 87410, off Barbados, in 300 m, 17.5 mm. 14–16. *Glyphostoma dentiferum* Gabb, 1872. Lectotype, ANSP IP2910, fossil, no data, 32.1 mm.

adapertural ribs almost reaching anterior end. Spiral sculpture of strong cords; cords developing heavy, spirally extended nodes as they cross axial elements; three cords on first whorl, progressively increasing to 6 by penultimate whorl; three peripheral cords strongest; a constricted band of strong, spirally extended nodes on anal fasciole appearing from earliest whorls; nodes not necessarily coinciding with axial cords, which are undercut by subsutural constriction; approximately 30 nodes on last whorl. Aperture (Figure 2) narrowly elongate, 12.2 mm in length, with short, tapering anterior canal slightly recurved to the right; outer lip strengthened by an abaperturally concave varix which terminates posteriorly in a deep, U-shaped sinus; varix crossed by 18 spiral cords, axially incised by a strong indentation which creates a secondary, thinner labrum; a third labral element, terminating in bifurcate denticles (broken at either side in the holotype), projects out of this secondary labral element (Figure 5). Inner labrum with 8 strong denticles; posterior denticle slightly stronger, slightly callused towards sinus. Parietal wall (Figure 2) with a moderately strong, nodulose callus at sinus entrance; central parietal wall with a small posterior denticle, followed by two strong plaits that continue into the inner aperture, an anterior bifurcate denticle, and a series of barely discernible nodes. Shell color white, with a pale-yellow peripheral band the width of 3 spiral cords on apical whorls and 5 on last whorl; a second sub-peripheral band on last whorl; coloration somewhat stronger in interstices.

**Type Material:** Holotype USNM 1274997, length 23.2 mm; width 8.8 mm (Figures 1–6). Paratype USNM 1274998, length 17.2 mm, width 7.1 m (Figures 7–8).

**Type Locality:** West of Dry Tortugas, SW Florida: 25°31.091' N, 84°28.391' W to 25°27.939' N, 84°27.145' W; in 352–361 m.

**Distribution:** Southwest of Key West to west of Dry Tortugas, southern Florida, in 84–361 m.

**Habitat:** *Glyphostoma coronaseminale* new species inhabits relatively deep water. The holotype was dredged in a sand bottom with broken shells. Other key species dredged in the same haul were a live specimen of *Bathyymota viabrunnea* Dall, 1889 and empty specimens of *Bartschia frumari* Garcia, 2008.

**Etymology:** A compound word from the Latin *corona* and *seminale* ("crown of seeds"); in reference to the characteristic spiral row of nodules that is present at the anal fasciole.

## DISCUSSION

The paratype of *Glyphostoma coronaseminale* (Figures 7–8) is bleached out, faintly showing the color bands; its central parietal wall shows the posterior denticle, the two subsequent plaits, and the anterior denticle, but the following anterior nodes are stronger than those of the holotype. As the latter was inhabited by a hermit crab, the weaker

nodes may be a result of erosion. The varical structure of the labrum of the paratype shows the same three stages of growth as the holotype, including the thinner, but strong, bifurcate denticles at the edge.

The specimens identified as *Glyphostoma golfoyaquense* Maury, 1917 in Kaicher's card 3882 (1984), and in Williams's (2005) image 5115 are *G. coronaseminale*. *Glyphostoma golfoyaquense* (Figures 9–10) is narrower, has fewer, wider axial ribs that become narrower and bifurcate at anterior half of last whorl, has a differently structured anal fasciole (Figure 10), and different dentition on parietal wall. The maximum reported size for *G. golfoyaquense* is 20 mm (Rosenberg, 2009).

The size, parietal dentition, and numerous, even-size axial ribs separate this new species from several other Western Atlantic *Glyphostoma*. *Glyphostoma pilsbryi* Schwengel, 1940, which inhabits waters of the Gulf of Mexico (García, 2007b) grows only to 9.5 mm, is relatively wider, and has fewer, thicker axial ribs. *Glyphostoma epicasta* Bartsch, 1934 has a more elongated, milky white shell with a longer siphonal canal, different structure of the anal fasciole, and different dentition on parietal wall. It grows larger than the new species, to a maximum reported size of 31 mm (Rosenberg, 2009). *Glyphostoma herminea* Bartsch, 1934 grows to a maximum size of 21 mm (Rosenberg, 2009), is yellowish white in coloration, has fewer, wider axial ribs, a more sloping, less constricted, differently sculptured anal fasciole, and different dentition on parietal wall.

The new species is most similar to *Glyphostoma gabii* (Dall, 1889) and *Glyphostoma dentiferum* Gabb, 1872. *Glyphostoma gabii* (Figures 11–13) has a wider aperture, fewer axial ribs that are narrower than the interspaces, a subsutural ornamentation of numerous arched axial riblets crossed by undulating spiral threads (Figure 13), axial cords on last whorl that bifurcate anteriorly, and different denticle structure on parietal wall (Figure 12). It has a maximum reported size of only 17.5 mm. *Glyphostoma dentiferum* (Figures 14–16) has fewer, stronger axial ribs on apical whorls, an anal fasciole sculptured with numerous arched axial riblets (Figure 16), differently structured denticles on parietal wall (Figure 15), and a longer siphonal canal. It grows larger than *G. coronaseminale*, with a maximum reported size of 32 mm (Rosenberg, 2009).

The bifurcated denticles of the projected third element of the labrum of *Glyphostoma coronaseminale* (Figure 5), have not been reported for any western Atlantic *Glyphostoma*. Notwithstanding the broken ends of this third element in the holotype, it is not at all fragile; the damage seems to have been cause by crab predation. It is possible that this third labral element is more fragile in other *Glyphostoma* species and has not been reported because of damage.

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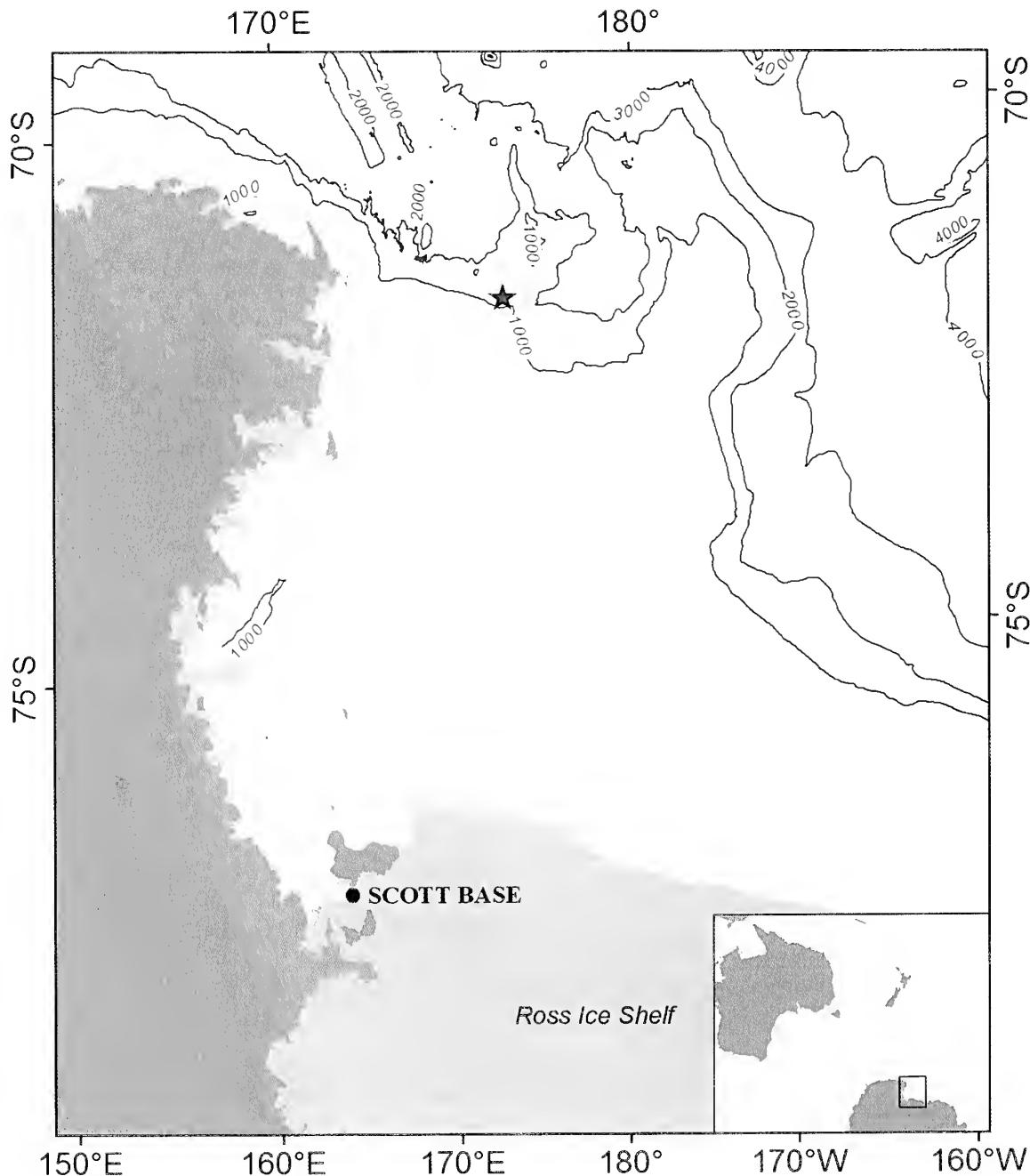
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## Research Note

### First evidence for deep-sea hot venting or cold seepage in the Ross Sea (Bivalvia: Vesicomyidae)

Two large dead valves of an undescribed clam of the family Vesicomyidae were recently collected by a toothfish (family Nototheniidae) longline vessel and returned to NIWA by a

Ministry of Primary Industries (MPI) observer. Using the Commission for the Conservation of Antarctic Marine Living Resources Identification Guide (CCAMLR 2009), the observer reported that the valves had a distinct sulphur smell, which, along with the location (Figure 1), suggests that the shells may have originated from or near an active seep and that living clams may still be there. The most complete valve (Figure 2) is very large (280 mm), and both



**Figure 1.** Location of vesicomyid clam sampled in the Ross Sea.



**Figure 2.** Vesicomyid clam from Ross Sea. Shell length = 280 mm.

are clearly old, blackish-stained, and with a sparse covering of encrusting bryozoans and calcareous polychaete tubes. Vesicomyid clams are found globally in chemosynthetic habitats using hydrogen sulfide for metabolism via symbiotic bacteria (Krylova and Moskalev, 1996; Krylova et al., 2010). While vent and seep species have been recorded previously from the Antarctic Region (Domack et al., 2005; Rogers et al., 2012), no vent or seep mollusks have been reported to date from the Ross Sea.

Apart from the enormous size, the Antarctic species is characterized by its exceptionally long ligament (length about 56% of shell length). In size, strongly posteriorly elongate shape, and general features of the shell, it most closely resembles some species of *Abyssogena* Krylova, Sahling, and Janssen, 2010, particularly *A. phaseoliformis* (Metivier, Okutani, and Ohta, 1986) and “*Ectenagena*” *extenta* (Krylova and Moskalev, 1996) (lengths up to 180 mm and 235 mm: Krylova et al., 2010). These species have been found, respectively, in the Japan, Kurile, and Aleutian trenches at 4550–6329 m, the Gulf of Alaska, the Monterey Canyon, the Kurile Trench, and the Costa Rica subduction zone at 3000–4445 m. Both species are from cold seeps.

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We acknowledge MPI Observer Geoff Dolan for returning the clam valves, and Ashley Rowden, Steve Parker, and David Bowden (NIWA) for comments. We thank Kevin Mackay (NIWA) for preparing Figure 1 and Jean-Claude Stahl (Te Papa) for preparing the images in Figure 2.

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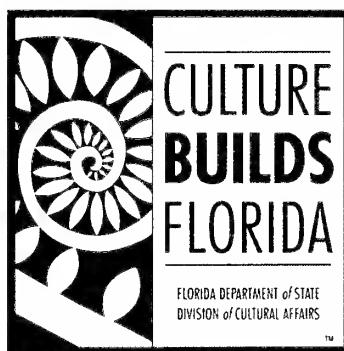
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Wellington 6011, NEW ZEALAND  
BruceM@tepapa.govt.nz

#### Di Tracey

National Institute of Water and Atmospheric Research (NIWA)  
Wellington 6021, NEW ZEALAND



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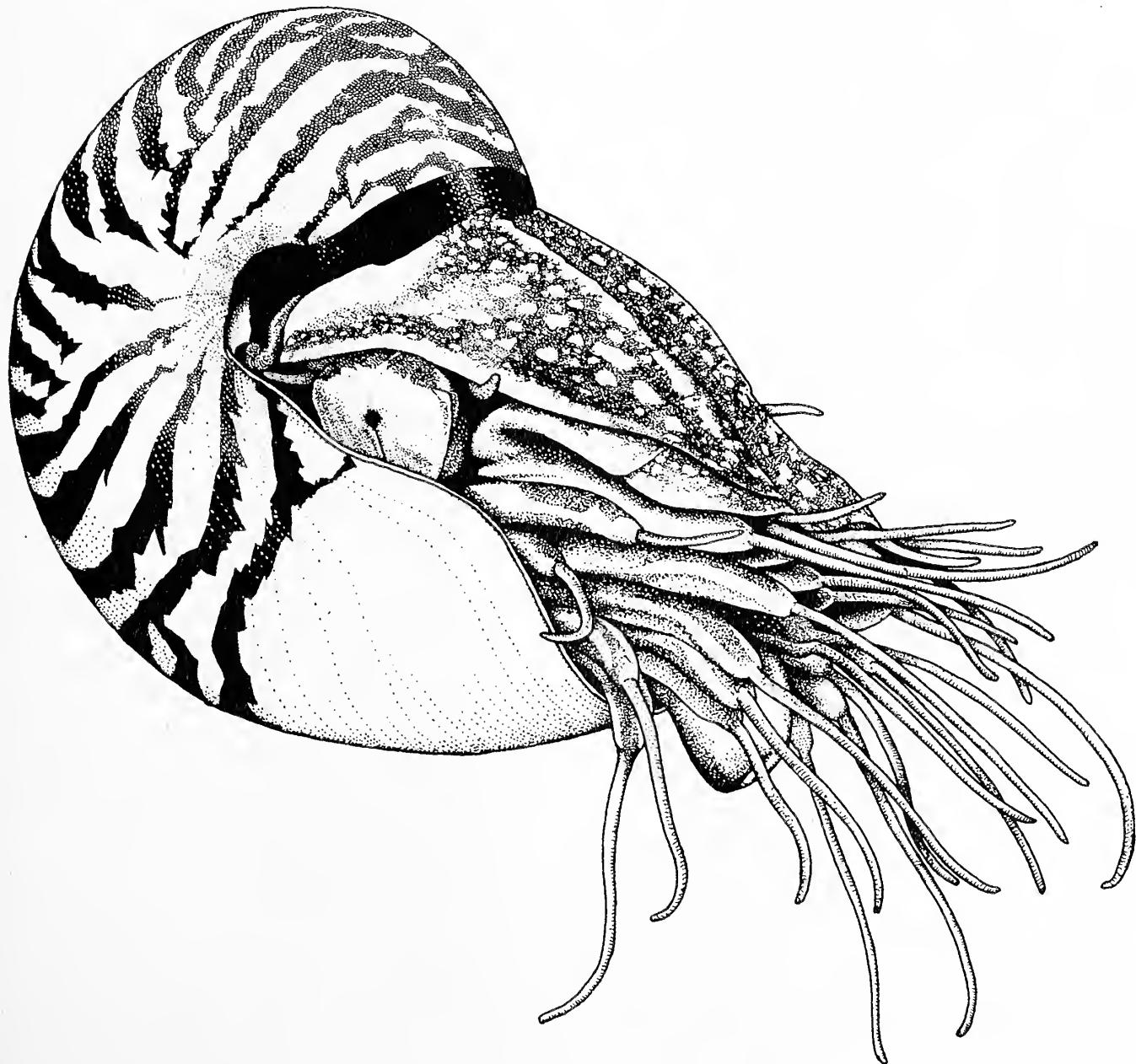
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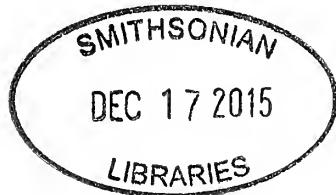
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# Four new species of Muricidae (Gastropoda) from New Caledonia, Papua New Guinea, and Indonesia

Roland Houart<sup>1</sup>

Institut royal des Sciences naturelles de Belgique  
Rue Vautier, 29  
B-1000 Bruxelles, BELGIUM  
roland.houart@skynet.be

## ABSTRACT

Four new species of Muricidae are described from New Caledonia, Papua New Guinea and Indonesia and compared with related species. One *Timbellus* species was collected in New Caledonia. Two other species are described from Papua New Guinea, respectively in *Chicopinnatus* and *Dermomurex*. The fourth species, also belonging in *Chicopinnatus*, originates from Indonesia.

*Additional Keywords:* Muricoidea, *Chicoreus*, *Timbellus*, *Dermomurex*

## INTRODUCTION

Many species have been traditionally classified in *Pterynotus* Swainson, 1833 and 16 species are currently considered as valid for this genus in WoRMS (Bouchet et al., 2015). However, according to recent molecular research (Barco et al., 2010), *Pterynotus* as traditionally defined (Vokes, 1964; 1971; Fair, 1976; Radwin and D'Attilio, 1976; Houart, 1994), appears to be polyphyletic consisting of at least two independent lineages. One group includes all the species with a sculptural pattern similar to the type species of *Pterynotus*, *P. alatus* (Röding, 1798) (= *Murex pinnatus* Swainson, 1822). A second group, based on the position in the molecular phylogeny of *P. fulgens* Houart, 1988, includes species generally classified in *Pterynotus* sensu stricto, but with a less scabrous shell sculpture and with three major axial varices “appearing early during the ontogeny” (Merle et al., 2011). The genus *Timbellus* was reinstated by Merle et al. (2011) to include the species that were formerly classified in *Pterynotus* but which differ in having a trivariate smooth rather than scabrous shell.

Eight species of *Timbellus* species are known from the New Caledonian area, six of them originally described in *Pterynotus* (Houart, 1987; 1988; 1991; 2001). Two addi-

tional species, formerly confused with *Timbellus richeri* (Houart, 1986), were recently separated and described as new *Timbellus* species (Houart, 2012). A ninth species is described here.

Species of *Chicopinnatus* Houart, 1992, a subgenus of *Chicoreus*, have been variously classified in *Pterynotus* sensu stricto and other genera. *Chicopinnatus* originally included three species: *Chicoreus* (*Chicopinnatus*) *orchidiflorus* (Shikama, 1973) (type species), *C. (C.) laqueatus* (Sowerby, 1841) and *C. (C.) guillei* (Houart, 1985). Different shell characters separate them from other genera and from *Chicoreus* sensu stricto. In this article, three additional species formerly included in *Pterynotus* or in *Timbellus* are added to *Chicopinnatus* and two new species are described from Papua New Guinea and Indonesia.

*Dermomurex* Monterosato, 1890 was organized by Vokes (1976) into five subgenera: *Dermomurex*, *Gracilimurex* Thiele, 1929, *Takia* Kuroda, 1953, *Triatella* Berry, 1964, and *Viator* Vokes, 1974. All these but *Gracilimurex* occur in the Indo-West Pacific. A new species from Papua New Guinea is described here but its classification in *Dermomurex* sensu stricto or *D. (Triatella)* is doubtful, as it shares shell characters of both subgenera. The new species is described without allocation to a subgenus.

## MATERIALS AND METHODS

The material in this paper originates from four sources. (1) The PAPUA NIUGINI expedition (Principal Investigator: Philippe Bouchet) conducted by MNHN and Pro-Natura International (PNI) as part of the *Our Planet Reviewed* program; its sponsors include the Total Foundation, Prince Albert II of Monaco Foundation, Stavros Niarchos Foundation, Fondation EDF, and Entrepose Contracting. The project operated under a Memorandum of Understanding between MNHN and the University of Papua New Guinea, with permits from the PNG Department of Environment and Conservation. The expedition took place along the coast of New Guinea Island in the Bismarck Sea, from the Vitiaz Strait to the border between Papua New Guinea and Irian Jaya; (2) The EXBODI

<sup>1</sup> Research Associate

cruise (Principal Investigator: Sarah Samadi) as part of the *Tropical Deep-Sea Benthos* program conducted by MNHN and Institut de Recherche pour le Développement (IRD); (3) The MUSORSTOM 4 cruise (Principal Investigator: Bertrand Richer de Forges), in northern and southern New Caledonia. Leg one of the latter expedition took place between 12 September and 5 October 1985 off northern and southern New Caledonia. Leg two took place between 13 September and 01 October 2011 and explored seamounts of the Loyalty Ridge; (4) One additional new species originates from the personal collection of Benjamin Dharma, Indonesia.

The new species descriptions are based on all the examined specimens. The characters used to describe the shell morphology are the general aspect of the shell, its shape and size, color, shape of the spire and number of protoconch and teleoconch whorls, features of the protoconch, shape of the teleoconch whorls and features or form of the suture and of the subsutural band, of axial and spiral sculpture, the aperture and siphonal canal. When known, the characters of the operculum are also used.

All width measurements are taken with the spines included. Abbreviations are: DW: Warén dredge; IRD: Institut de Recherche pour le Développement (formerly ORSTOM); ORSTOM: Office de la Recherche Scientifique et Technique d'Outre Mer (now IRD); Collection abbreviations are: MNHN: Muséum national d'Histoire naturelle, Paris, France; MZB: Museum Zoologicum Bogoriense, Bogor, Java, Indonesia; RH: collection of the author; ZSM: Zoologischen Staatssammlung, München, Germany; Specimen status: dd: empty shell(s); juv: juvenile; lv: live collected.

**Terminology used to describe the spiral cords and apertural denticles, listed according to type of structure (after Merle, 2001 and 2005) (Terminology in parentheses: variable feature) (Figures 1–5):** **P:** primary cord; **s:** secondary cord; **t:** tertiary cord; **ad:** adapical; **ab:** abapical; **IP:** infrasutural primary cord (primary cord on subsutural ramp); **adis:** adapical infrasutural secondary cord (on subsutural ramp); **abis:** abapical infrasutural secondary cord (on subsutural ramp); **P1:** shoulder cord; **P2–P6:** primary cords of the convex part of the teleoconch whorl; **s1–s6:** secondary cords of the convex part of the teleoconch whorl; example: s1 = secondary cord between P1 and P2; s2 = secondary cord between P2 and P3, etc.; **ADP:** adapertural primary cord on the siphonal canal; **MP:** median primary cord on the siphonal canal; **ABP:** abapertural primary cord on the siphonal canal; **abs:** abapertural secondary cord on the siphonal canal; **Aperture, D1 to D6:** abapical denticles; **ID:** Infrasutural denticle.

## SYSTEMATICS

Family Muricidae Rafinesque, 1815  
Subfamily Muricinae Rafinesque, 1815

### Genus *Timbellus* de Gregorio, 1885

**Type Species:** *Murex latifolius* Bellardi, 1872, Middle Miocene, Italy (subsequent designation by Vokes, 1964: 14)

#### *Timbellus corbariae* new species

(Figures 1–2, 6–11)

**Description:** Shell medium sized for the genus, up to 39.6 mm in length at maturity (holotype). Length/width ratio of the holotype 1.56. Last whorl slender, triangular with variceal wings, whorls narrow, almost smooth, lightly built. Subsutural ramp broad, strongly sloping, weakly concave.

Light creamy white with scattered brown blotches on whorls and varices, more particularly visible in paratype. Aperture white. Spire high, acute, with 7 narrowly convex, weakly shouldered, almost smooth, teleoconch whorls. Suture impressed. Protoconch broken in the two specimens. Axial sculpture of teleoconch whorls consisting of 3 narrow, strongly webbed varices. Each varix bearing very thin, almost smooth, wing-like expansion from first to last whorl. Other axial sculpture of 2 or 3 narrow, nodose, intervariceal ribs, from suture to suture. Last whorl with 3 very low, narrow ribs, middle one weakly higher. Spiral sculpture of very weak, narrow, smooth, barely visible primary and secondary cords, most obvious on abapertural side of variceal wings. Paratype with P1–P3 visible from second whorl. Last whorl with adis, IP, abis, P1–P6, s6. No visible cords on siphonal canal.

Aperture small, ovate. Columellar lip moderately broad, smooth, adherent at adapical extremity. Anal notch deep, broad. Outer lip weakly erect, smooth with 7 strong, weakly elongate denticles within: ID, D1–D6, decreasing abapically in height and strength. Siphonal canal long, broad, straight, strongly dorsally bent at tip, with variceal wing over whole length, smooth. Operculum and radula unknown.

**Type Material:** Holotype MNHN IM-2000-30342 and 1 paratype MNHN (as listed below).

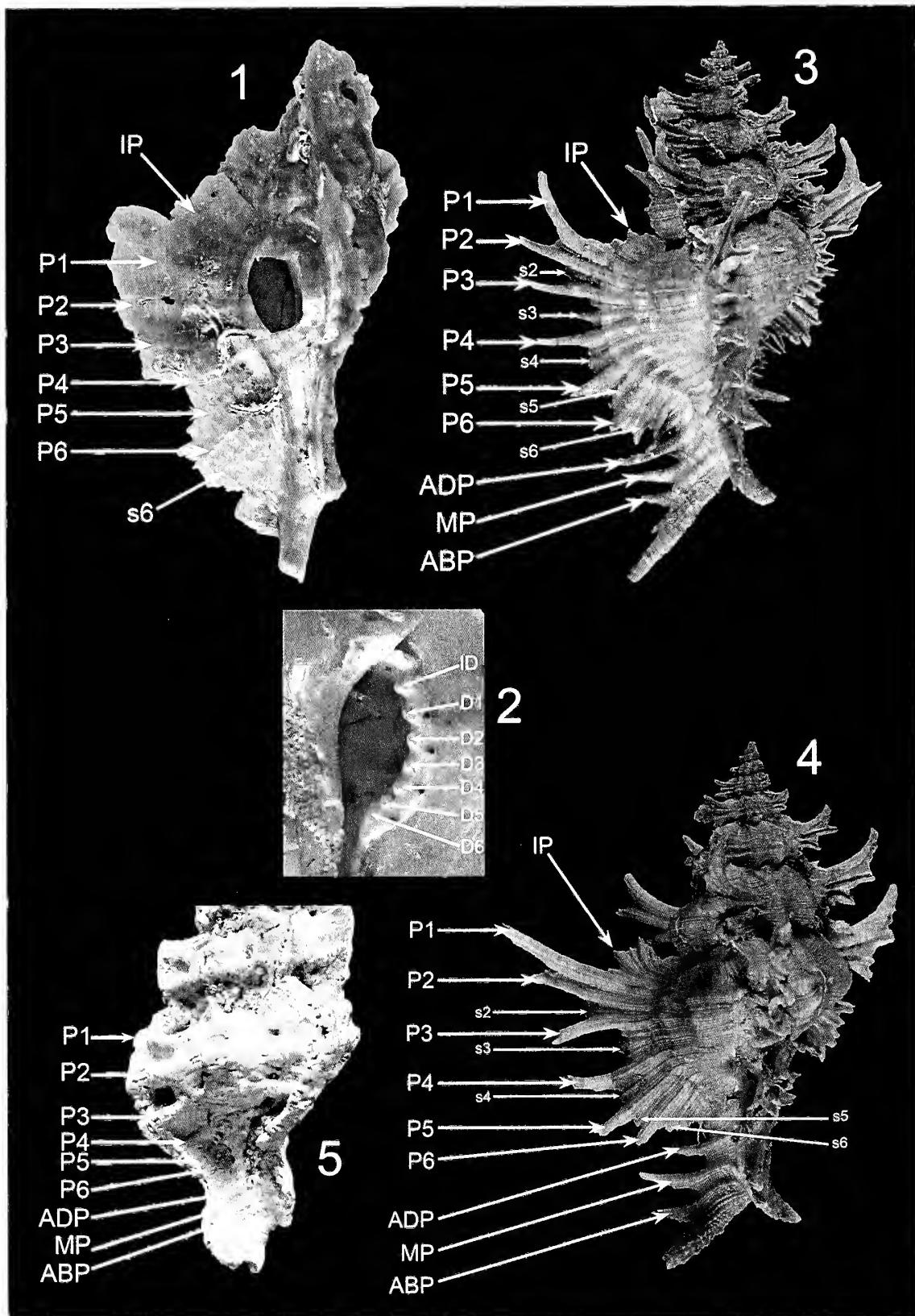
**Other Material Examined:** New Caledonia: EXBODI, stn DW3857, South Durand Bank, 22°18' S, 168°42' E, 342 m, 14 September 2011 (holotype) (dd); MUSORSTOM 4, stn DW205, 22°38' S, 167°07' E, 140–160 m, 27 September, 1985, 1 paratype MNHN IM-2000-30343 (dd).

**Type Locality:** New Caledonia, South Durand Bank, 22°18' S, 168°42' E, 342 m.

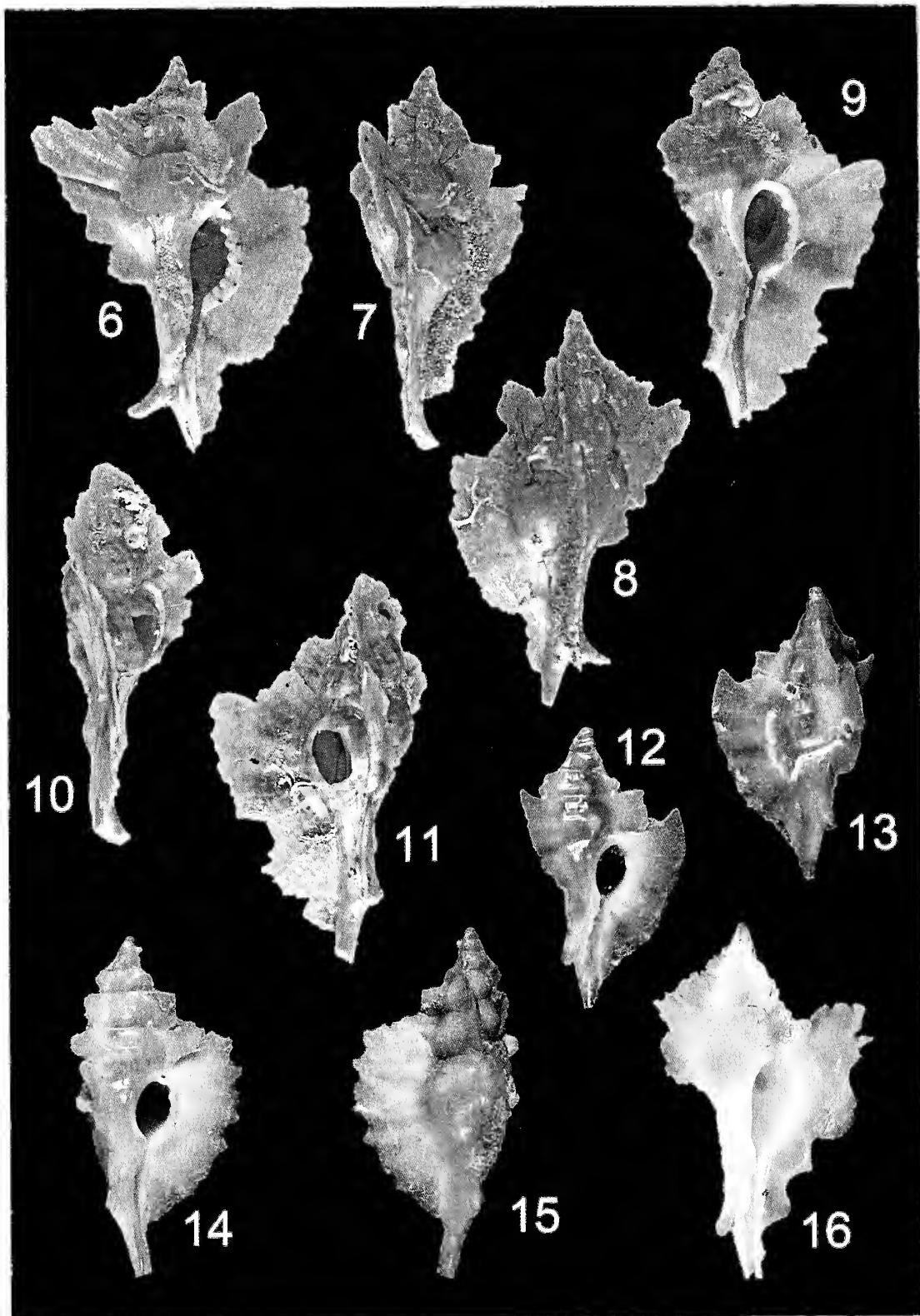
**Distribution:** South of New Caledonia, empty shells in 160–342 m.

**Remarks.** Eight species of *Timbellus* occur off New Caledonia and in the Coral Sea, living in deep water, mostly between 200 to 400 m. Only two of these can be reasonably compared with the new species.

*Timbellus corbariae* new species differs from *T. rubidus* Houart, 2001 (Figures 12–13) in having a larger shell. *Timbellus corbariae* has two additional teleoconch whorls,



**Figures 1-5.** New species of *Timbellus* and *Chicoreus*. Morphology of spiral cords and apertural denticles. 1-2. *Timbellus corbariae* new species. 1. Paratype MNHN IM-2000-30343. 2. Holotype MNHN IM-2000-30342. 3. *Chicoreus (Chicopinnatus) arbagui* new species. Holotype MNHN-IM-2013-14388. 4. *Chicoreus (Chicopinnatus) dharmai* new species. 5. *Dermomurex fitialeatai* new species. Holotype MNHN IM-2013-14300.



**Figures 6–16.** Species of *Timbellus*. **6–11.** *Timbellus corbariae* new species. **6–8.** New Caledonia, EXBODI, stn DW3857, South Durand Bank,  $22^{\circ}18' S$ ,  $168^{\circ}42' E$ , 342 m, holotype MNHN IM-2000-30342, 39.6 mm. **9–11.** New Caledonia, MUSORSTOM 4, stn DW205,  $22^{\circ}38' S$ ,  $167^{\circ}07' E$ , 140–160 m, paratype MNHN IM-2000-30343, 36.5 mm. **12–13.** *Timbellus rubidus* (Houart, 2001). New Caledonia, Norfolk Ridge,  $23^{\circ}44' S$ ,  $168^{\circ}16' E$ , 394–401 m, holotype MNHN-IM-2000-0346, 13.2 mm (photos MNHN). **14–15.** *Timbellus fulgens* (Houart, 1988). New Caledonia, 390–420 m,  $22^{\circ}52' S$  –  $167^{\circ}12' E$ , holotype MNHN-IM-2000-0082, 25.5 mm (photos MNHN). **16.** *Timbellus flemingi* (Beu, 1967). Norfolk Ridge, north of Norfolk Island, 750–774 m, RH, 28.7 mm.

which could explain its larger size, but the whorls are also larger and broader and have 2 or 3 low, narrow and elongate intervariceal ridges instead of a single, obvious, small node in *T. rubidus*, from first to last teleoconch whorl. The aperture in *T. corbariae* is also comparatively larger and broader and the spiral cords are obviously narrower and shallower on the variceal wings.

*Timbellus corbariae* differs from *T. fulgens* (Houart, 1988) (Figures 14–15) in having a larger shell and a comparatively larger aperture with more obvious, high, apertural denticles and in having 2 or 3 low intervariceal elongate ridges instead of an almost smooth shell in *T. fulgens*.

A third similar species is *T. flemingi* (Beu, 1967) (Figure 16) from New Zealand. *Timbellus corbariae* differs in having a more elongate shell instead of strongly biconical in *T. flemingi* and in having a higher spire. *Timbellus corbariae* differs further in having a broader aperture that is denticulate instead of almost or entirely smooth, and in having two or three intervariceal elongate nodes instead of a single low node or none.

**Etymology:** Named for Laure Corbari (MNHN), chief scientist during the second leg of the EXBODI campaign (13/9 to 01/10/2011) when the holotype was collected.

### Genus *Chicoreus* Monfort, 1810

#### Subgenus *Chicopinnatus* Houart, 1992

**Type Species:** *Pterynotus orchidiflorus* Shikama, 1972, Indo-West Pacific (original designation).

**Remarks:** Three species are currently included in this subgenus: *Chicoreus (Chicopinnatus) orchidiflorus* (Shikama, 1972) (Figures 49–50), *C. (C.) guillei* (Houart, 1985), and *C. (C.) laqueatus* (Sowerby, 1841).

Five additional species are added here: *C. (C.) brianbaileyi* (Mühlhäuser, 1984), *C. (C.) loebbeckei* (Kobelt, 1879), *C. (C.) miyokoae* (Kosuge, 1979), *C. (C.) arbaguil* new species and *C. (C.) dharmai* new species.

*Chicoreus (Chicopinnatus) miyokoae* was tentatively included in *Timbellus* (Merle et al., 2011: 133) and *C. (C.) brianbaileyi* in *Pterynotus* (Merle et al., 2011: 121). Both species are similar in shell morphology and, together with *C. loebbeckei* and the two new species described here, share similar shell characters with *Chicopinnatus*, such as the rounded or roundly ovate aperture, the moderately long, spined siphonal canal, the more or less webbed variceal spines and the trivaricate morphology starting from first teleoconch whorl.

*Chicopinnatus* species differ from *Pterynotus alatus* (Röding, 1798) (= *Murex pinnatus* Swainson, 1822), the type species of the genus *Pterynotus* and from *P. albobrunneus* Bertsch and D'Attilio, 1980, *P. elongatus* (Lightfoot, 1786), *P. laurae* Houart, 1997, *P. patagiatus* (Hedley, 1912) and *P. pellucidus* (Reeve, 1845) in having a broader shell with broader, round or roundly ovate aperture, a comparatively narrower siphonal canal, a lower, broader spire and a trivaricate shell starting from

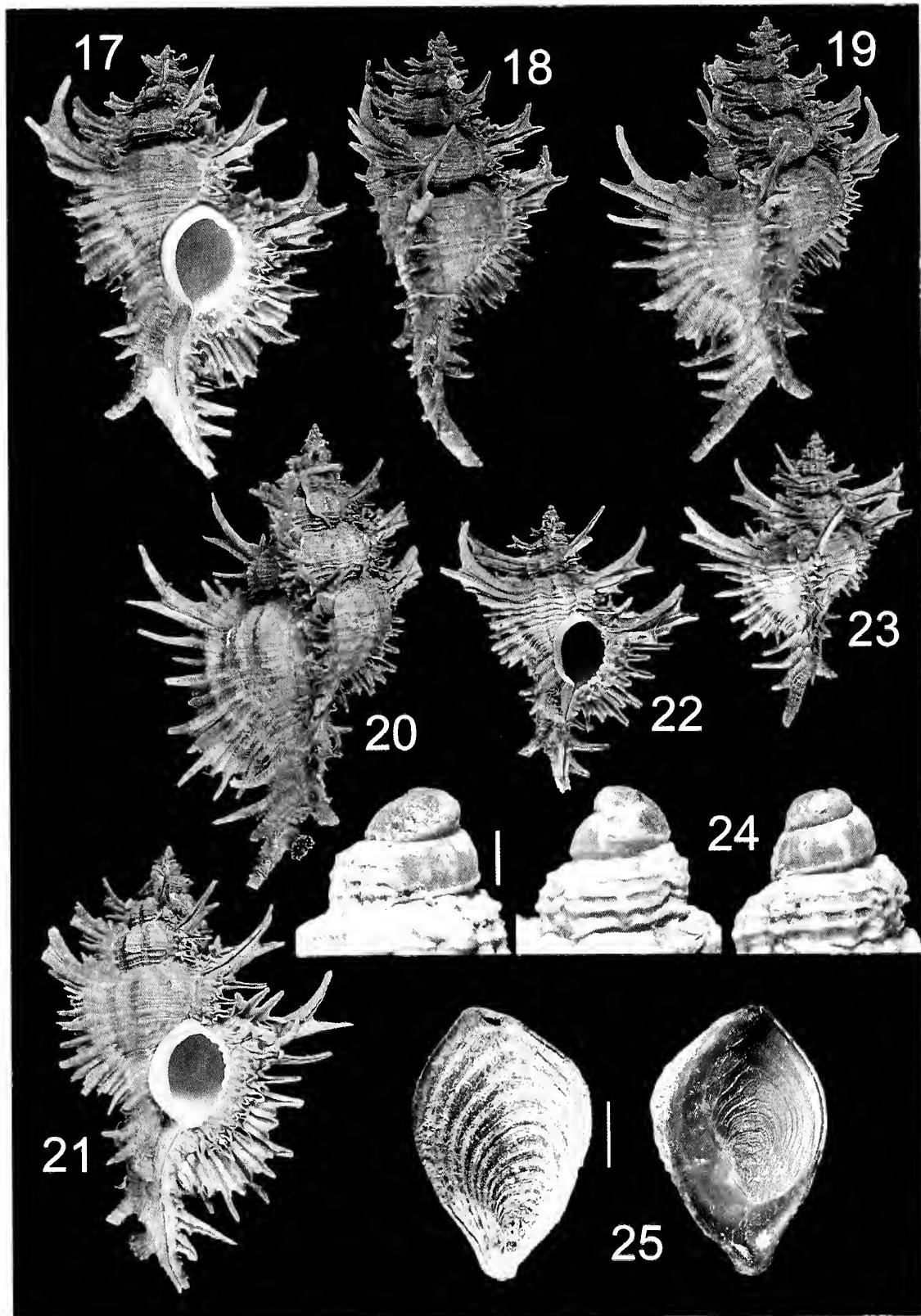
first teleoconch whorl rather than from second or third whorl in *Pterynotus*.

*Chicopinnatus* species differ further from *Timbellus* species in having a broader shell with broader, more rounded aperture but mainly in having a squamous shell compared to the smooth, or almost smooth shell in *Timbellus*.

A molecular phylogenetic study of the whole group is necessary to test this new classification.

#### *Chicoreus (Chicopinnatus) arbaguil* new species (Figures 3, 17–25, 34)

**Description:** Shell large for the subgenus, up to 85.9 mm in length at maturity (paratype MNHN IM-2013-14446). Length/width ratio 1.21–1.51. Biconical, broadly ovate, heavy, strongly spinose, nodose. Subsutural ramp narrow, weakly sloping, convex. Light brown or tan, occasionally with light purplish spinose fronds (holotype). Primary and secondary cords lightly darker colored. Apertural side of siphonal canal lighter colored. Aperture white. Spire high with 2 protoconch whorls and teleoconch up to 8 broad, weakly shouldered, spinose and nodose whorls. Suture impressed. Protoconch small, weakly flattened, with rounded whorls. Last whorl minutely punctate, with a narrow, strong keel abapically. Width 1300 µm, height 1100 µm (paratype MNHN IM-2000-30344). Terminal lip almost straight, partly eroded. Axial sculpture of teleoconch whorls consisting of high, narrow, rounded, nodose varices. Each varix with long, acute, open, webbed, primary, secondary and tertiary spines. Shoulder spine longest. P1–P3 and P4–s6 spines joined by thin webbing. Other axial sculpture of high, strong, rounded intervariceal ribs. First teleoconch whorl already starting 3 small, rounded varices with 2 or 3 intervariceal narrow ribs; second whorl with intervariceal ribs becoming broader. Three varices and 2 or 3 broad, high, intervariceal ribs from fourth to last whorl. Spiral sculpture of high, narrow, squamous and nodose primary, secondary and tertiary cords and few, nodose, narrow threads. First whorl with visible P1–P4; second whorl starting IP; third and fourth with adis, IP, P1, P2, P3, s3, P4; fifth with adis, IP, abis, P1, P2, P3, s3, P4, starting additional threads; seventh whorl of subadult paratype MNHN IM-2000-30344 with adis, IP, abis and 2 additional threads on subsutural ramp, followed by P1, P2, P3, s3, P4, s4, P5, s5, P6, s6, tertiary cords and few threads. Siphonal canal with strongly backward curved ADP, straight MP and ABP. P1 and P2 spines joined by thin webbing from third to last whorl, including P3 spine from fifth to last whorl. S3 not joined to other spines. P4 to s6 spines webbed. Adult shell with 8 teleoconch whorls having similar shell sculpture morphology. Aperture large, broadly ovate. Columellar lip narrow, smooth, with low parietal tooth at adapical extremity. Rim adherent at adapical extremity, weakly erect abapically. Anal notch shallow, broad. Outer lip erect, crenulated, with strong, low, narrow lirae within: IP split, D1, D2–D7 occasionally split. Siphonal canal long, narrow, lightly



**Figures 17–25.** *Chicoreus (Chicopinnatus) arbagil* new species. **17–19.** Papua New Guinea, PAPUA NIUGINI, stn PP06, Rempi area, east of Tadwai Island, 145°48' E, 04°59' S, 180 m, holotype MNHN IM-2013-14388, 83.3 mm. **20–21.** stn PP07, Rempi area, east of Tadwai Island, 145°48' E, 04°59' S, 150 m, paratype MNHN IM-2013-14446, 85.9 mm. **22–23.** Madang Lagoon, no other data, paratype MNHN IM-2000-30344, 44.1 mm. **24.** Protoconch (paratype MNHN IM-2000-30344), scale bar 500  $\mu$ m. **25.** Operculum (holotype IM-2013-14388), scale bar 500  $\mu$ m.

abaxially bent, weakly dorsally recurved at tip, narrowly open, with 3 or 4 acute spines: ADP, MP, ABP, (abs), decreasing in length abapically. Operculum dark brown, broadly ovate, with subapical nucleus and 13 concentric ridges. Attached surface with many growth lines and broad, callused rim. Radula unknown.

**Type Material:** Holotype MNHN IM-2013-14388 (lv) and 3 paratypes MNHN, 1 coll. RH (as listed below).

**Material Examined: Papua New Guinea:** PAPUA NIUGINI, stn PP06, Rempi area, east of Tadwai Island, 145°48' E, 04°59' S, 180 m, 19 November 2012, 1 lv (holotype IM-2013-14388); stn PP07, Rempi area, east of Tadwai Island, 145°48' E, 04°59' S, 150 m, 20 November 2012, 1 lv (paratype MNHN IM-2013-14446); Madang Lagoon, November–December 2012, no other data, 2 paratypes MNHN IM-2000-30344 (1 lv, 1 dd, juv), 1 paratype RH (dd).

**Type Locality:** Papua New Guinea, Rempi area, east of Tadwai Island, living at 180 m.

**Distribution: Papua New Guinea:** Rempi area, east of Tadwai Island, living at 150–180 m and Madang Lagoon, no other data.

**Remarks:** *Chicoreus (Chicopinnatus) arbaguil* differs from *C. brianbaileyi* (Figures 36–43) in having a larger, more elongate shell with a same number of teleoconch whorls, a comparatively larger and broader aperture, and less expanded variceal wings with longer spines. It also has a comparatively higher spire and a longer siphonal canal with more broadly spaced spiral cords. The distance between P4 and ADP is more reduced with less webbed wings and narrower spiral cords. The protoconch (Figure 24) is smaller with broader first whorl and a strongly keeled last whorl compared to the broader, smooth protoconch of *C. brianbaileyi* (Figure 43).

*Chicoreus (Chicopinnatus) arbaguil* differs from *C. miyokoae* (Figures 44–46) in having a more elongate and larger shell with a same number of teleoconch whorls, more broadly spaced spiral cords, and broader primary cords. The spire is higher, the siphonal canal longer and the ADP, MP and ABP cords are not webbed like in *C. miyokoae*. The aperture is comparatively larger. The variceal spines are longer, straight and not short, strongly webbed and adaperturally recurved as in *C. miyokoae*. The protoconch is almost twice as wide with a strongly keeled last whorl while it is small and smooth in *C. miyokoae* (Figure 46).

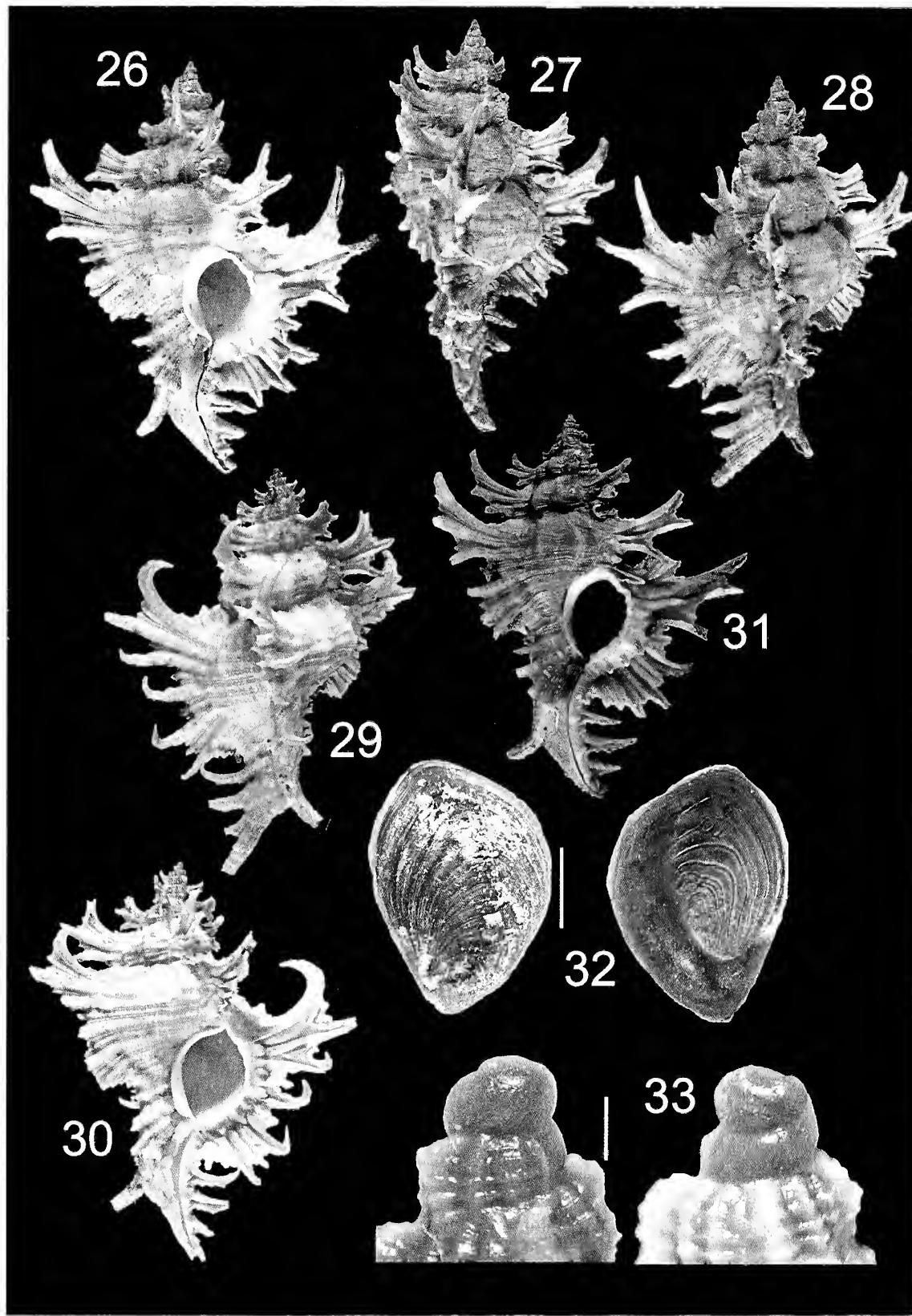
*Chicoreus (Chicopinnatus) arbaguil* differs from *C. loebbeckei* (Figures 47–48) by the same characters separating it from *C. miyokoae*. *Chicoreus (Chicopinnatus) arbaguil* differs further in having lecithotrophic larval development, as attested by the paucispiral, rounded protoconch, rather than planktotrophic development as in *C. loebbeckei*, which has a conical protoconch of more than three whorls with a narrow keel abapically and a terminal lip of sinusigera type (Figure 48).

**Etymology:** This new *Chicoreus* is named after Jo Arbasto and Noel Saguil who, during the Madang expedition, operated the tangle nets that led to its discovery. Jo Arbasto is a professional tangle net fisherman on the island of Panglao, in the Philippines, and Noel Saguil has been a project officer working for biodiversity projects, also in the Philippines. Both contributed immensely to the success of MNHN expeditions, notably the Panglao and Aurora expeditions in the Philippines, Santo 2006 in Vanuatu, and now the Papua New Guinea Madang 2012 expedition. The word *arbaguil* is used as a noun in apposition.

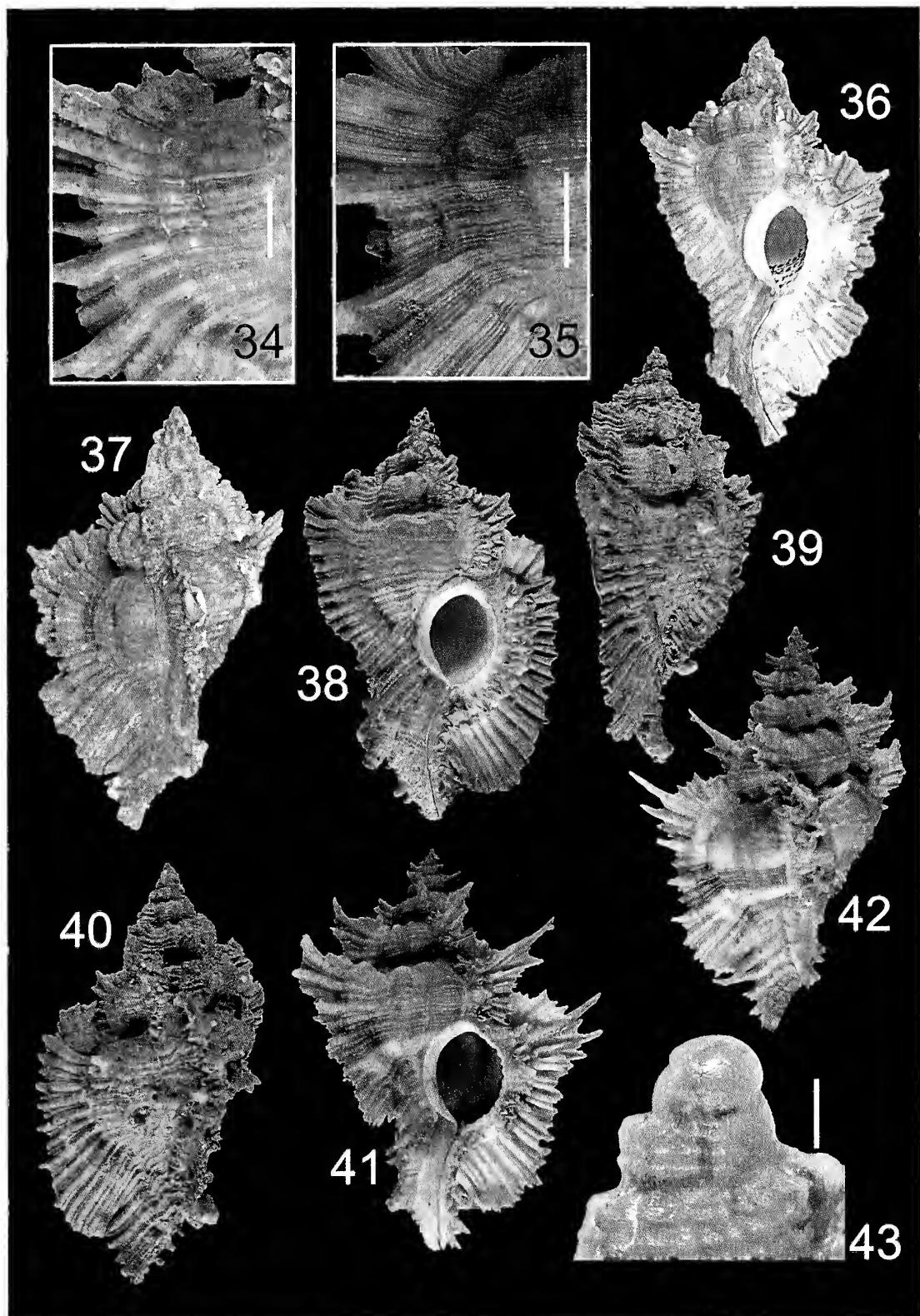
***Chicoreus (Chicopinnatus) dharmai* new species**  
(Figures 4, 26–33, 35)

*Pterynotus brianbaileyi*.—Dharma, 2005: 164, pl. 57, fig. 14 (not *Pterynotus brianbaileyi* Mühlhäuser, 1984).

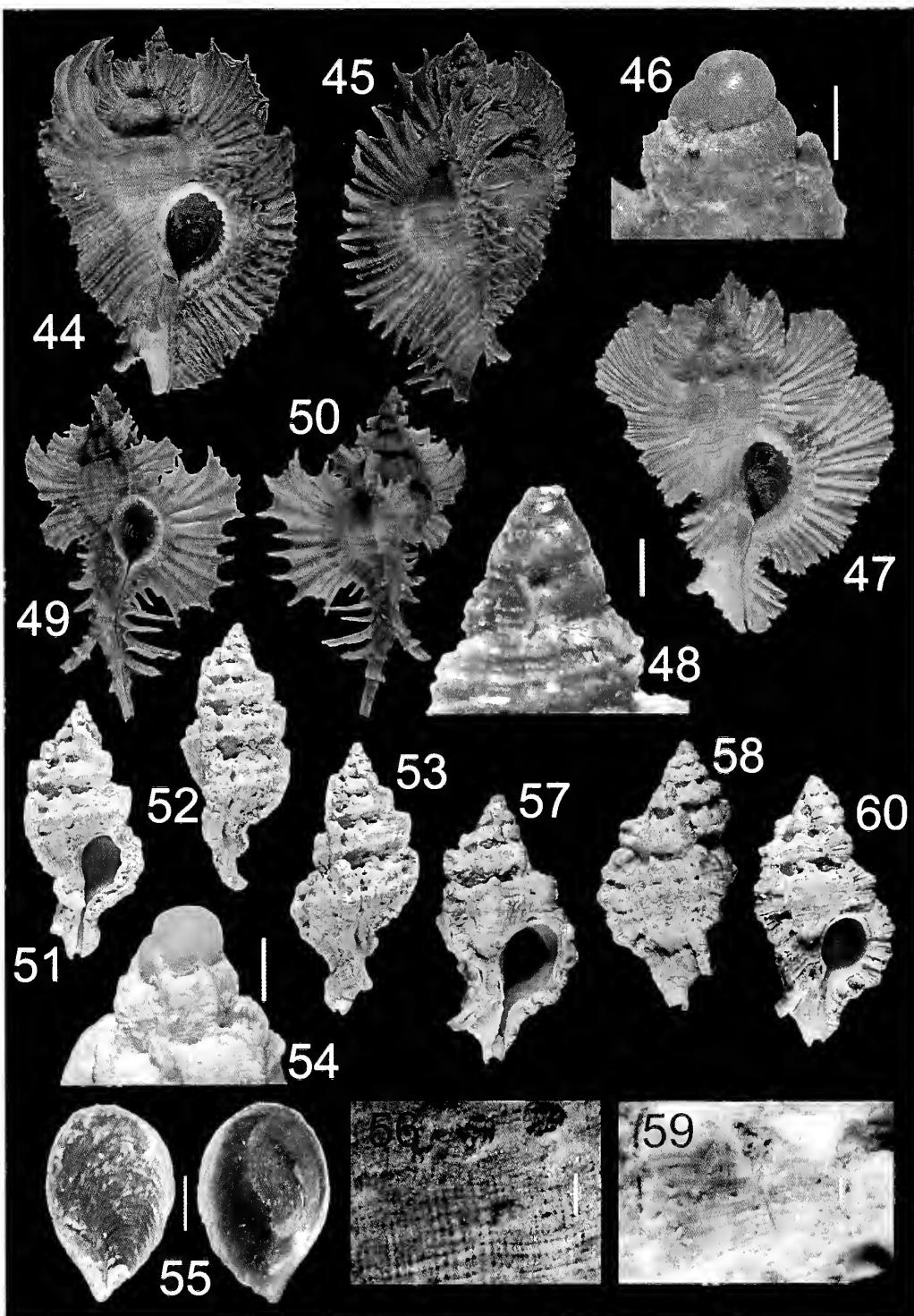
**Description:** Shell large for the subgenus, up to 74.6 mm in length at maturity (holotype). Length/width ratio 1.25–1.26. Biconical, broad, heavy, spinose and nodose. Subsutural ramp broad, weakly sloping and convex. White or light tan with pinkish or brown protoconch and 2 or 3 first teleoconch whorls. Primary, or primary and secondary cords topped with narrow brown line. Aperture white. Spire high with 2 protoconch whorls and teleoconch up to 8 broad, weakly shouldered, spinose and nodose whorls. Suture impressed. Protoconch small, whorls rounded, smooth. Maximum height and width 1300 µm. Terminal lip almost straight, partly eroded. Axial sculpture of teleoconch whorls consisting of high, narrow, rounded, nodose varices. Each varix with long, broad, open, webbed, primary and short secondary spines. Shoulder spine longest. P1–P3 and P4–s6 spines joined by thin webbing. First whorl already starting 3 small, rounded varices with 2 or 3 nodose intervariceal ribs; third whorl with broader ribs. Fourth to last whorl with 2 broad, high, intervariceal ribs. Spiral sculpture of low, narrow, nodose, primary, secondary and tertiary cords and numerous nodose threads. First whorl with visible IP, P1–P4; second with IP, P1, P2, P3, s3, P4; third whorl starting spiral threads; fourth to penultimate whorl with visible adis, IP, abis, P1, P2, P3, s3, P4. Last whorl with adis, IP, abis, P1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6, two additional tertiary cords and numerous spiral threads over whole shell. Siphonal canal with almost straight or straight ADP, MP and ABP. P1 and P3 spines webbed from second to last whorl; P4 to s6 spines webbed. S3 not joined by webbing to other spines. Aperture large, broadly ovate. Columellar lip narrow, smooth, with low parietal tooth at adapical extremity. Rim adherent at adapical extremity, weakly erect abapically. Anal notch shallow, broad. Outer lip erect, crenulated, with strong, low, narrow lirae within: IP split, D1, D2–D7 occasionally split. Siphonal canal long, narrow, lightly bent abaxially, weakly dorsally recurved at tip, narrowly open, with 3 acute, straight or almost straight spines: ADP, MP, ABP, decreasing in length abapically. Operculum dark brown, broadly ovate, with subapical nucleus and 17 concentric ridges (paratype B, Dharma).



**Figures 26–33.** *Chicoreus (Chicopinnatus) dharmai* new species. **26–28.** Indonesia, East Java, Banyuwangi-Jember, 146 m, in lobster nets, holotype MZB Gst. 18174, 74.5 mm. **29–30.** Lombok Island, in lobster net,  $\pm$  91 m, paratype RH, 67.3 mm. **31.** East Java, Muncar, 165 m, in lobster nets, paratype B. Dharma, 65.8 mm. **32.** Operculum (paratype B. Dharma), scale bar 500  $\mu$ m. **33.** Protoconch (paratype RH), scale bar 500  $\mu$ m.



**Figures 34–43.** Species of *Chicoreus*. 34–35. Spiral sculpture (scale bar 5 mm). 34. *Chicoreus (Chicopinnatus) arbaguil* new species, holotype MNHN-IM-2013-14388. 35. *Chicoreus (Chicopinnatus) dharmai* new species, paratype RH. 36–43. *Chicoreus (Chicopinnatus) brianbaileyi* (Mühlhäusser, 1984). 36–37. Russell Island, Solomon Islands, holotype ZSM 1746, 74 mm (photo E. Schwabe). 38–40. Solomon Islands, SALOMONBOA3, stn DW2855, 9°45' S, 160°50' E, 183 m, MNHN IM-2009-5858, 67.2 mm. 41–42. Vanuatu, MUSORSTOM 8, stn CP1071, 15°37' S, 167°16' E, 180–191 m, MNHN-IM-2012-18002, 62.6 mm. 43. Protoconch, scale bar 500  $\mu$ m.



**Figures 44–60.** Species of *Chicoreus* and *Dermomurex*. **44–46.** *Chicoreus (Chicopinnatus) miyokoae* (Kosuge, 1979). **44–45.** Philippines, Sainal, Ligid Island, 58.5 mm, RH. **46.** Protoconch. Philippines, Davao, RH, scale bar 500  $\mu$ m. **47–48.** *Chicoreus (Chicopinnatus) loebbeckei* (Kobelt, 1879). Philippines, Davao, Samal Island, 53.6 mm, RH. **48.** Protoconch, scale bar 500  $\mu$ m. **49–50.** *Chicoreus (Chicopinnatus) orchidiflorus* (Shikama, 1972). Philippines, Bohol, Caubian Island, 130 m, RH, 41.6 mm. **51–56.** *Dermomurex fitialeatai* new species. **51–53.** Papua New Guinea, north of Tadwai Island, outer slope, 145°47.7'E, 04°59.1'S, 22 m, holotype MNHN IM-2013-14300, 18.9 mm. **54.** Protoconch (holotype), scale bar 500  $\mu$ m. **55.** Operculum (holotype), scale bar 1 mm. **56.** Detail of the intritacalx (holotype), scale bar 1 mm. **57–59.** *Dermomurex triclotae* Houart, 2001. **57–58.** New Caledonia, channel of Koumac pass, 20°40.7' S, 164°14.7' E, holotype MNHN-IM-2000-0340, 13.10 mm (photo MNHN). **59.** Detail of the intritacalx (paratype RH), scale bar 1 mm. **60.** *Dermomurex trondleorum* Houart, 1990, French Polynesia, Tuamotu Archipelago, Anaa Atoll, holotype MNHN-IM-2000-0223, 17 mm (photo MNHN).

Attached surface with many growth lines and broad, callused rim. Radula unknown.

**Type Material:** Holotype MZB Gst. 18174, 1 paratype B. Dharma; 1 paratype collection RH (as listed below).

**Material Examined: Indonesia:** East Java, Bamyuwangi-Jember, 146 m, in lobster net, January 2014, 1 dd (holotype MZB); East Java, Muncar, 165 m, in lobster net, 1 lv (paratype coll. B. Dharma); Lombok Island, in lobster net, about 90 m, 2005, 1 dd (paratype coll. RH).

**Type Locality:** Indonesia, East Java, Bamyuwangi-Jember, 146 m, in lobster nets.

**Distribution:** Indonesia, east of Java and Lombok Island, living at 165m.

**Remarks:** *Chicoreus (Chicopinnatus) dharmai* is similar to *C. arbaguil* but differs in protoconch and other shell morphology. The protoconch is comparatively larger, higher and smooth rather than flatter and having a strongly keeled last whorl in *C. arbaguil*. The sculpture of the teleoconch is also similar but the spiral cords are narrower in *C. dharmai*, and the spiral threads are more numerous (Figures 34–35), IP starts from first teleoconch whorl rather than the second and the space between cords P4 and s6 is distinctly narrower (Figures 3–4). The shell is also stockier than *C. arbaguil*, smaller for a same number of teleoconch whorls, and has a lower spire and a notably shorter siphonal canal with straight rather than strongly backward curved ADP spine.

*Chicoreus (Chicopinnatus) dharmai* differs from the other more or less similar species, *C. brianbaileyi*, *C. miyokoae* and *C. loebbeckei* in having more strongly spinose axial varices, lower and narrower intervariceal nodes, less numerous, narrower secondary spiral cords and a comparatively narrower and longer siphonal canal.

I earlier misidentified a specimen of *C. dharmai* as *C. brianbaileyi* which was thus identified as such by Dharma (2005).

**Etymology:** This species is named for Benjamin Dharma, who kindly donated the holotype and in acknowledgement for more than 20 years of useful collaboration.

### Genus *Dermomurex* Monterosato, 1890

**Type Species:** *Murex scalarinus* Bivona-Bernardi, 1832 (= *Murex scalaroides* Blainville, 1829), Mediterranean Sea and Eastern Atlantic (Senegal) (original designation).

**Remarks:** There are currently fifteen Recent Indo-West Pacific species assigned to *Dermomurex* Monterosato, 1890. Six belong in *Dermomurex* sensu stricto: *D. agnesae* Vokes, 1995, *D. angustus* (Verco, 1895), *D. charlesi* Houart and Héros, 2013, *D. goldsteini* (Tenison Woods, 1876), *D. neglecta* (Habe and Kosuge, 1971), and *D. raywalkeri* Houart, 1986; four in subgenus *Takia* Kuroda, 1953: *D. africanus* Vokes, 1978, *D. bobyini* Kosuge, 1984, *D. infrons* Vokes, 1974, and *D. wareni* Houart, 1990; two in subgenus *Trialatella* Berry, 1964: *D. triclotae* Houart,

2001 and *D. trondleorum* Houart, 1990; and three in subgenus *Viator* Vokes, 1974: *D. antonius* Vokes, 1974, *D. howletti* Vokes, 1995, and *D. pasi* Vokes, 1993.

A simple key to separate the subgenera of *Dermomurex* was given by Vokes (1985):

#### I. SPIRE SHORT

A Six varices

1. Moderate canal
2. Long, straight canal

B Three varices

#### II. SPIRE ELONGATE

A Two varices

B Three to six varices

*Takia*

*Viator*

*Trialatella*

*Gracilimurex*

*Dermomurex* sensu stricto

Although the distinction between *Dermomurex* sensu stricto, *Dermomurex* (*Takia*), and *Dermomurex* (*Viator*) is clear, it is not readily apparent how to separate some species of *Dermomurex* sensu stricto from *Dermomurex* (*Trialatella*). For example, the species newly described here could be allocated into *Trialatella* because it has three axial varices per whorl from third to last teleoconch whorl, but the spire is elongate rather than short as in *Trialatella* and fits better in *Dermomurex* sensu stricto. Other representatives of uncertain relationship were recorded by Merle et al. (2011: 212–213), who also doubted the need for *Trialatella*. Therefore the decision was taken here to describe this new species without any subgeneric distinction.

### *Dermomurex fitialeatai* new species

(Figures 5, 51–56)

**Description:** Shell medium sized for the genus, 18.9 mm in length. Length/width ratio 2.35. Slender, lanceolate, nodose, lightly built. Subsutural ramp narrow, weakly sloping and convex. Shell covered by thick, white, minutely reticulate intritacalx. Aperture bluish-white. Spire high with 1.5 protoconch whorls and 6.5 weakly convex, narrow, shouldered, nodose whorls. Suture impressed, partially obscured by small, narrow buttresses connecting preceding whorl. Protoconch small. Whorls rounded, smooth, height 900 µm, width 800 µm. Terminal lip lightly erect, narrow, opisthocline. Axial sculpture of teleoconch whorls consisting of narrow lamellae and high, strong, narrow, rounded varices. First and second whorl with 6 axial lamellae; third whorl starting varices. Three rounded varices and one narrow, low, intervariceal node from fourth to last whorl. Spiral sculpture of low, rounded, broad, nodose, primary cords, visible from fourth to last whorl. Last whorl with P1–P6. P1, P2 and P3 broad, moderately high, more obvious when connecting axial varices, forming deep pits between P1 and P2 and P2 and P3. P4, P5 and P6 almost obsolete, probably more obvious when intritacalx removed. Siphonal canal with very low ADP, MP and ABP. Aperture small, ovate. Columellar lip narrow, smooth, adherent. Anal notch shallow, broad. Outer lip not fully adult, smooth within. Siphonal

canal short, narrow, dorsally bent at tip, open. Operculum dark brown, roundly ovate, inverted tear-shaped with apical nucleus and numerous concentric ridges. Attached surface with about 4 growth lines and very broad, large, callused rim. Radula unknown.

**Type Material:** Holotype MNHN IM-2013-14300 (lv).

**Material Examined: Papua New Guinea:** PAPUA NIUGINI, stn PB26, north of Tadwai Island, outer slope, 145°47,7'E, 04°59,1'S, 22 m, 22 November 2012 (holotype MNHN).

**Type Locality:** Papua New Guinea, north of Tadwai Island, outer slope, 145°47,7' E, 04°59,1' S, 22 m.

**Distribution:** Papua New Guinea, north of Tadwai Island, living at 22 m.

**Remarks.** *Dermomurex fitialeatai* new species can only be compared with *D. triclotae* Houart, 2001 from New Caledonia (see discussion under *Dermomurex*). It differs from all the other species in having a trivaricate shell whereas the other species from the Indo-West Pacific bear four to six varices.

*Dermomurex trondleorum* from French Polynesia also has a trivaricate shell but differs in many ways and does not need to be compared further here. It is only illustrated for reference (Figure 60).

*Dermomurex fitialeatai* new species differs from *D. triclotae* (Figures 57–59) in having a more elongate spire, 7 varices on first teleoconch whorl and 6 on second and third, while decreasing from 6 varices on first whorl to 3 on all the subsequent whorls in *D. triclotae*. The intritacalx also differs in being minutely reticulate in *D. fitialeatai* (Figure 56) and faintly striate in *D. triclotae* (Figure 59).

**Etymology:** The name of this species is dedicated to Christian Késiano Fitialeata, who tragically passed away during the first leg of BioPapua, another expedition to Papua New Guinea, which took place in 2010.

## ACKNOWLEDGMENTS

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# On the phylogenetic relationships of the genus *Mexistrophia* and of the family Cerionidae (Gastropoda: Eupulmonata)

**M.G. Harasewych**

**Amanda M. Windsor**

Dept. of Invertebrate Zoology, MRC-163  
National Museum of Natural History  
Smithsonian Institution  
PO Box 37012  
Washington, DC 20013-7012 USA  
Harasewych@si.edu

**Estuardo Lopez-Vera**

Instituto de Ciencias del Mar y Limnología  
Universidad Nacional Autónoma de México  
Círculo Exterior S/N  
Ciudad Universitaria  
Delegación Coyoacán  
CP: 04510 Mexico D.F. MEXICO

**Fred G. Thompson**

Florida Museum of Natural History  
University of Florida  
Gainesville, FL 32611 USA

## ABSTRACT

Phylogenetic analyses of partial DNA sequences of the mitochondrial CO1 and 16S rDNA genes derived from *Mexistrophia reticulata* Thompson, 2011, the type species of the genus *Mexistrophia*, indicate that this genus is sister taxon to all remaining living Cerionidae, and that the family Cerionidae is most closely related to Urocoptidae. Relationships among representative cerionid taxa are consistent with the zoogeographic hypothesis that *Mexistrophia* has been isolated from the remaining living Cerionidae since the Cretaceous, and suggest that the near-shore, halophilic habitat that has commonly been associated with this family is likely a Cenozoic adaptation that coincided with the transition from continental to island habitats. The genus *Protocerion* is described to include the Late Cretaceous species *Cerion acherontis* Roth and Hartman, 1998, as its retention in *Cerion* would render this genus paraphyletic.

## INTRODUCTION

The family Cerionidae comprises a well-studied group of terrestrial snails inhabiting islands of the tropical western Atlantic, ranging from the barrier islands of southeastern Florida, throughout the Bahamas, Greater Antilles, Cayman Islands, western Virgin Islands, and the Dutch Antilles, but absent from Jamaica, the Lesser Antilles, and coastal Central and South America. All are halophilic, confined to terrestrial vegetation growing in close proximity of the shore, but occasionally occur further inland in areas that can be reached by salt spray (Clench, 1957; Woodruff, 1978). Rare fossil taxa extend the range of Cerionidae to the Upper Cretaceous of Montana (Roth and Hartman, 1998) and the Paleocene of the Itaboráí Basin of Brazil (Salvador et al., 2011). More recently, the genus *Mexistrophia* was proposed within the Cerionidae to include three new species inhabiting cool coniferous forests in the highlands (2000–2600 m) of central Mexico (Thompson, 2011). Thompson (2011) compared the shell

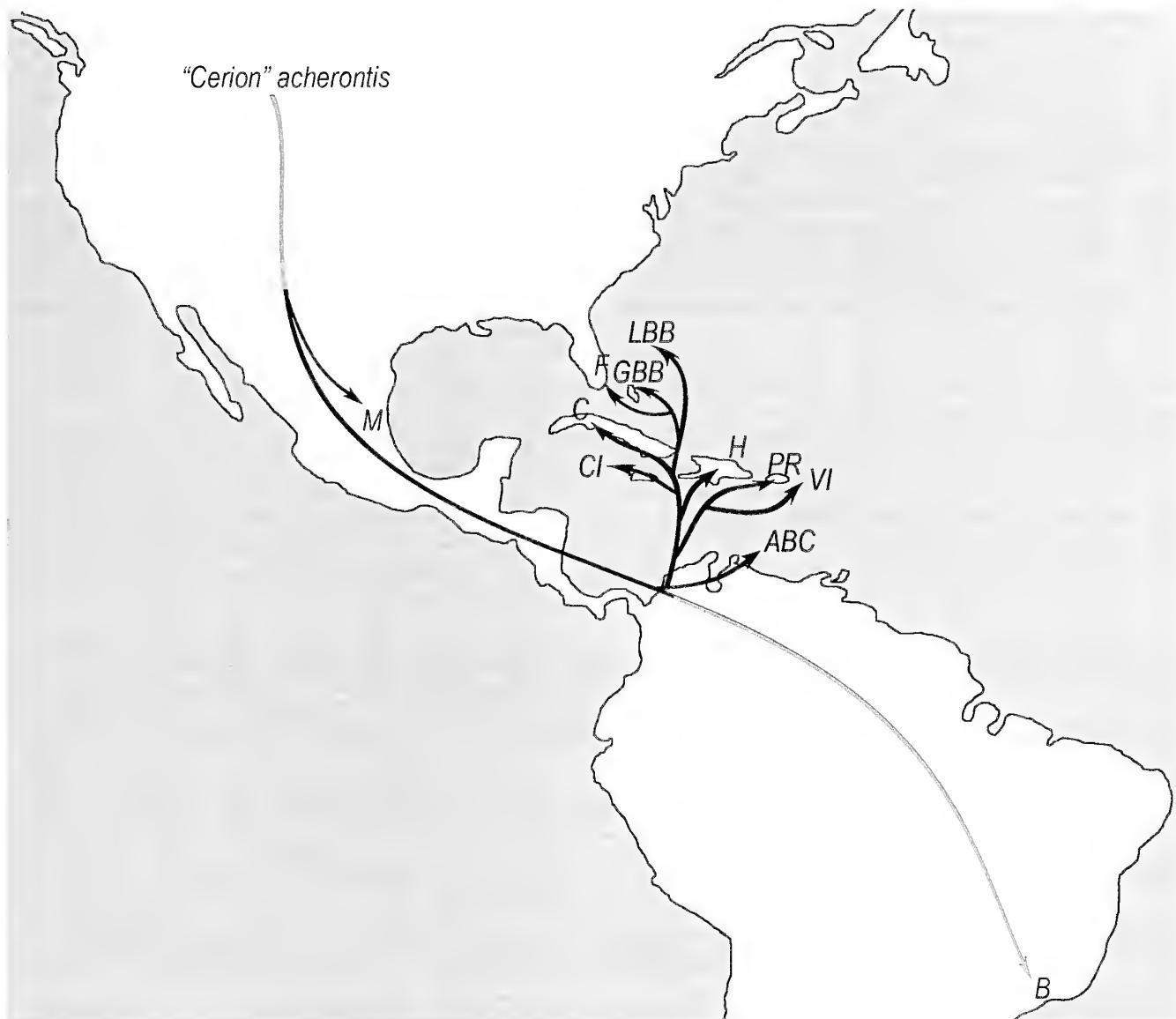
morphology, anatomy, and radula of *Mexistrophia reticulata*, the type species of *Mexistrophia*, with those of several species of *Cerion*, including *Cerion uva* (Linnaeus, 1758), the type species of the type genus of Cerionidae. He concluded that anatomical features of *Mexistrophia reticulata* are typical of Cerionidae and that radular morphology differs only slightly. However, *Mexistrophia* may be distinguished from species of *Cerion* in lacking lamellae and denticles along the columella at all stages of growth.

Harasewych (2012) reviewed the diversity of living and fossil Cerionidae from geographic and temporal perspectives and combined these data with paleogeographic reconstructions of the Caribbean region (Iturralde-Vinent, 2006) and a COI based phylogeny of a selection of cerionid taxa (Harasewych et al., 2011: fig. 17) to formulate a hypothesis for the zoogeographic history of the family Cerionidae from the earliest fossil record in the Late Cretaceous of Montana to the more widespread modern fauna. According to this hypothesis (Figure 1), *Mexistrophia* was an early offshoot that was isolated from the South American ancestors of all remaining cerionids during the Late Cretaceous by the formation of a seaway separating the faunas of North and South America.

The family Cerionidae has been assigned to a variety of superfamilies, among them Orthalicoidea (Thiele, 1931; Bouchet et al., 2005) Clausilioidea (Baker, 1961; Solem, 1978; Tillier, 1989) Cerioidea (Baker, 1955; Shileyko, 1979, 1999) and most recently Urocoptoidea (Uit de Weerd, 2008). In this paper we investigate the phylogenetic relationships of the genus *Mexistrophia* to other members of the Cerionidae as well as the placement of the family Cerionidae within Eupulmonata based on partial sequences for the COI and 16S genes.

## MATERIALS AND METHODS

Specimens of *Mexistrophia reticulata* Thompson, 2011 were collected west of Pinal de Amoles, Querétaro State, Mexico (21°07' 26.52" N, 99°40'59.58" W), not far from the type locality for this species. The shells were cracked,



**Figure 1.** Hypothesized zoogeographic history of the family Cerionidae (after Harasewych 2012:fig. 12). Grey portions based on fossil taxa. ABC, Aruba, Bonaire and Curaçao; B, Brazil; C, Cuba; CI, Cayman Islands; F, Florida; GBB, Great Bahama Bank; H, Hispaniola; LBB, Little Bahama Bank; M, Mexico; PR, Puerto Rico, VI, western Virgin Islands.

and the animals preserved in RNAlater and stored at  $-70^{\circ}\text{C}$  (voucher material USNM 1283835). As the Cerionidae had most recently been included in Urocoptidea on the basis of molecular data (Uit de Weerd, 2008), tissue from living specimens of *Microceramus pontificus* (Gould, 1848) from South Miami, Florida (voucher specimens USNM 1283834) were also sequenced in order to include a member of the family Urocoptidae in this analysis.

Genomic DNA was extracted from buccal muscle dissected from preserved or living specimens using the DNAeasy Tissue Kit (Qiagen) according to the manufacturer's animal tissue protocol.

Portions of two mitochondrial genes were amplified: a 655 bp region of the cytochrome c oxidase I gene using the primers JgLCO1490 (Geller et al., 2013) and C1-N-

2191R (aka NancyCOIR) (Simon et al., 1994) and a 510 bp region of the 16S ribosomal gene using the primers 16S-ar and 16S-br (Palumbi, 1996). For each gene, the Promega GoTaq hot start master mix (Promega M7132) was utilized at concentrations according to manufacturer's instructions, but modified to reduce reaction volume to 20  $\mu\text{L}$ . Cycling parameters for each gene region were optimized as follows: COI – initial denaturation for 7 min at  $95^{\circ}\text{C}$  + 45 cycles (30 sec at  $95^{\circ}\text{C}$  + 45 sec at  $42^{\circ}\text{C}$  + 1 min at  $72^{\circ}\text{C}$ ) + 3 min at  $72^{\circ}\text{C}$ ; 16S – initial denaturation for 7 min at  $95^{\circ}\text{C}$  + 35 cycles (30 sec at  $95^{\circ}\text{C}$  + 45 sec at  $48^{\circ}\text{C}$  + 1 min at  $72^{\circ}\text{C}$ ) + 5 min at  $72^{\circ}\text{C}$ . PCR products were visualized by agarose gel electrophoresis (1.5% agarose) and purified with ExoSAP-IT (Affymetrix) according to manufacturer's protocols prior to sequencing.

Sequencing reactions for 16S were performed using 1  $\mu$ L of purified PCR product in a 10  $\mu$ L reaction containing 0.5  $\mu$ L primer, 1.75  $\mu$ L Big Dye buffer and 0.5  $\mu$ L Big Dye (Life Technologies); for COI the volume of Big Dye was increased to 0.75  $\mu$ L. The sequencing reaction was carried out under standard cycling conditions (25 cycles of 5 sec at 95 °C + 10 sec at 50 °C + 4 min at 60 °C). Reactions were purified using Millipore Sephadex plates (MAHVN-4550) according to the manufacturer's instructions and sequenced on an ABI 3730XL automated DNA sequencer. Sequencher v. 4.7 (GeneCodes, Ann Arbor, MI, USA) was used to visualize, trim, edit, and assemble contigs from forward and reverse sequences. All PCR, sequencing, and analytics were carried out at the Laboratories of Analytical Biology at the National Museum of Natural History. The sequences have been deposited in GenBank (NCBI). Accession numbers are listed in Table 1.

Partial sequences for the mitochondrial COI and 16S genes of *Mexistrophia reticulata* and *Microceramus pontificus* were aligned against a range of euhyneuran taxa for which both COI and 16S sequences were available (Table 1), most derived from complete mitochondrial

genomes. Representative species of Cerionidae were selected to span the previously documented phylogenetic diversity within the family (Harasewych et al., 2011: fig. 17).

Alignments of COI and 16S were obtained using the L-INS-i alignment strategy in MAFFT (Katoh et al., 2002) for 16S and MUSCLE (Multiple Sequence Comparison by Log-Expectation) (Edgar, 2004) for COI. The aligned sequences were concatenated using Geneious version 7.1.2 (Kearse et al., 2012). In the concatenated data set, positions 1-554 are 16S, and positions 555 to 1212 are COI.

A best-fit model of nucleotide sequence evolution (compatible with MrBayes) and partitioning arrangement for each locus was determined using MrAIC (Nylander, 2004). The GTR+I+G model was chosen for both loci.

Phylogenetic analyses were performed on a concatenated dataset (16S + COI) using Bayesian Inference (BI) performed with MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) and Maximum Likelihood (ML) with RAxML (Stamatakis, 2006). All analyses were run on the Smithsonian Institution high performance computing cluster (SI/HPC). BI analysis was carried out for 10 million

**Table 1.** List of taxa and their GenBank reference numbers for the gene sequences used in phylogenetic analyses. Asterisk (\*) denotes that both COI and 16S sequence data were derived from a complete mitochondrial genome sequence.

Taxon	COI GenBank No.	16S GenBank No.	Superfamily	Family
<b>Euhyneura</b>				
<b>Euopisthobranchia</b>				
<i>Aplysia californica</i>	NC005827*		Aplysioidea	Aplysiidae
<b>Panpulmonata</b>				
<i>Siplonaria pectinata</i>	AY345049*		Siphonarioidea	Siphonariidae
<i>Salinator rhamphidia</i>	JN620539*		Amphiboloidea	Amphibolidae
<b>Hygrophila</b>				
<i>Biomphilaria glabrata</i>	AY380531*		Planorbioidea	Planorbidae
<i>Physella acuta</i>	NC023253*		Planorbioidea	Physidae
<i>Galba pertia</i>	JN564796*		Lymnaeoidea	Lymnaeidae
<b>Eupulmonata</b>				
<i>Ovatella vulcani</i>	JN615139*		Ellobioidea	Ellobiidae
<i>Trimusculus reticulatus</i>	JN632509*		Trimusculoidea	Trimusculidae
<i>Platevindex mortoni</i>	GU475132*		Onchidioidae	Onchidiidae
<i>Onchidella celtica</i>	NC012376*		Onchidioidae	Onchidiidae
<i>Peronia peronii</i>	JN619346*		Onchidioidae	Onchidiidae
<i>Vertigo pusilla</i>	NC026045*		Pupilloidea	Vertiginidae
<i>Gastrocopta cristata</i>	KC185403*		Pupilloidea	Pupillidae
<i>Pupilla muscorum</i>	NC026044*		Pupilloidea	Pupillidae
<i>Albinaria caerulea</i>	X83390*		Clausilioidea	Clausiliidae
<i>Achatina fulica</i>	NC024601*		Achatinoidea	Achatinidae
<i>Camaena cicatricosa</i>	NC025511*		Helicoidea	Camaenidae
<i>Mastigeulota kiangsinensis</i>	NC024935*		Helicoidea	Bradybaenidae
<i>Cylindrus obtusus</i>	JN107636*		Helicoidea	Helicidae
<i>Cepaea nemoralis</i>	CMU23045*		Helicoidea	Helicidae
<i>Helix aspersa</i>	JQ417194*		Helicoidea	Helicidae
<i>Microceramus pontificus</i>	KT272166	KT272164	Urocoptoidea	Urocoptidae
<i>Mexistrophia reticulata</i>	KT272165	KT272163	Urocoptoidea	Cerionidae
<i>Cerion uva</i>	KJ624975	KJ636144	Urocoptoidea	Cerionidae
<i>Cerion striatellum</i>	KJ934716	KJ636083	Urocoptoidea	Cerionidae
<i>Cerion malonei</i>	KJ934718	KJ636085	Urocoptoidea	Cerionidae
<i>Cerion stevensoni</i>	KJ934720	KJ636087	Urocoptoidea	Cerionidae
<i>Cerion caerulescens</i>	KJ934722	KJ636089	Urocoptoidea	Cerionidae
<i>Cerion incanum</i>	NC025645*		Urocoptoidea	Cerionidae

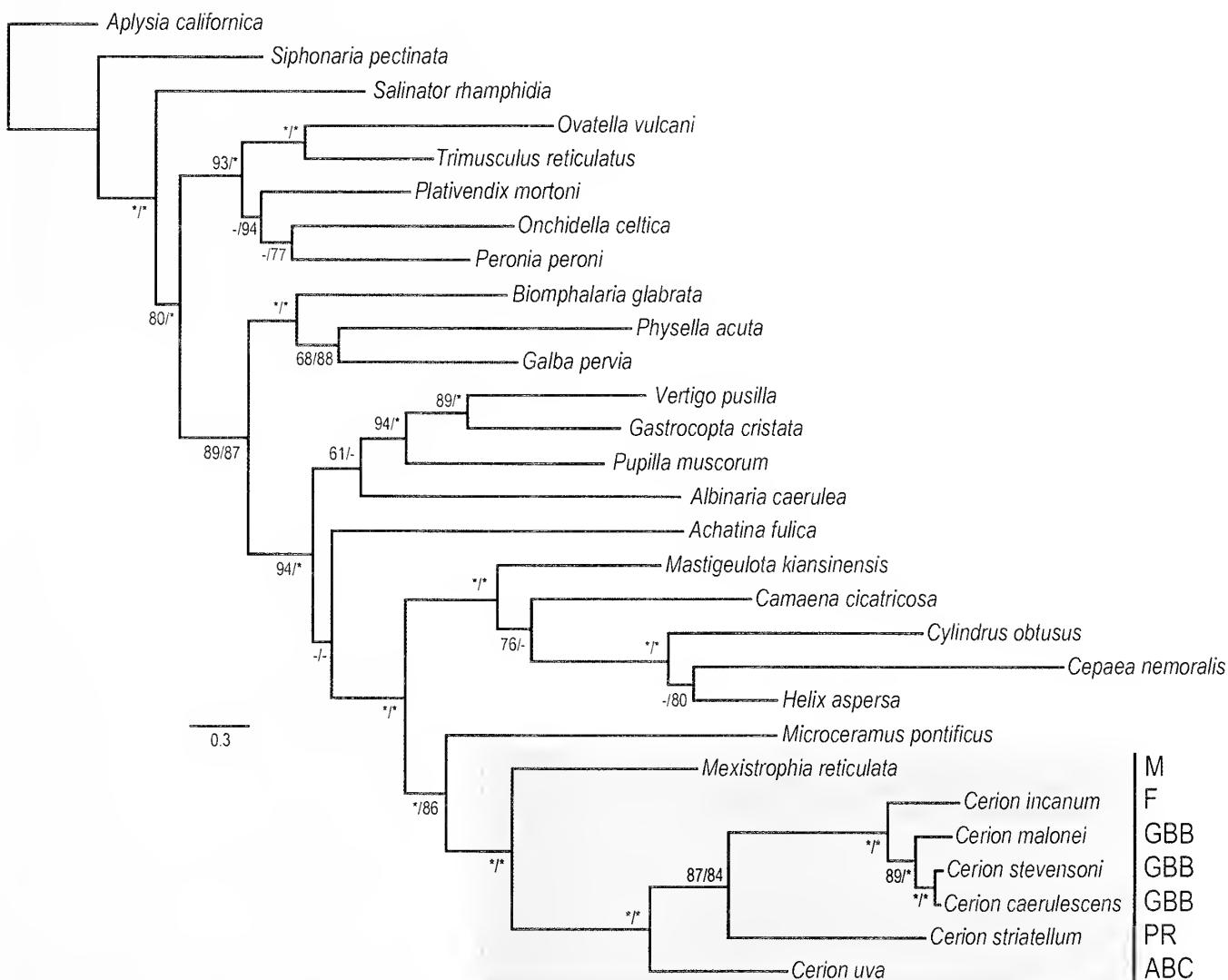
generations with two independent runs, each with four chains, and with trees sampled every 1000th generation. Model parameters (tratio, statefreq, shape, pinvar) were unlinked among partitions, and the rate prior (prset ratepr) was set to “variable”. Convergence was determined when the average standard deviation of split frequencies was  $<0.01$  and the potential scale reduction factor (PSRF) was 1.00. To calculate posterior probabilities, a “burn-in” of 25% of the total trees sampled per run adequately removed trees prior to convergence. ML options for RAxML included the GTRCAT model of nucleotide evolution (-m), rapid bootstrap analysis, and search for best-scoring ML tree (-f a), and 1000 bootstrap replicates.

## RESULTS

The region of the 16S gene sequenced for *Mexistrophia reticulata* and *Microceramus pontificus* corresponded

to positions 564–1069 of the 16S gene in *Cerion incanum*. The length was 486 bp in *Mexistrophia* and 476 bp in *Microceramus*. The alignment containing the taxa in Table 1 spanned 554 positions, of which 174 (31.4%) were constant and 326 (58.8%) were parsimony informative. The 655 bp portion of the COI gene sequenced for *Mexistrophia reticulata* and *Microceramus pontificus* corresponded to positions 39–693 of the COI gene in *Cerion incanum*. The COI alignment of the taxa in Table 1 spanned 658 bp, of which 310 (47.1%) were constant and 302 (45.9%) were parsimony informative.

Phylogenetic analyses of the concatenated 16S + COI data using maximum likelihood and Bayesian inference resulted in a single, fully resolved and well supported tree (Figure 2). *Mexistrophia* emerged as the sister taxon to all remaining living Cerionidae, and the family Cerionidae as sister taxon to the single representative



**Figure 2.** Molecular phylogenetic tree from analyses of concatenated 16S and COI sequence data, represented as a maximum likelihood phylogram with maximum likelihood bootstrap values/ Bayesian posterior probabilities. (\*  $\geq 95\%$  support, -  $\leq 50\%$  support). The family Cerionidae is in gray. Letters to the right of the bar correspond to the geographic localities / island groups identified in figure 1.

of the family Urocoptidae. Cerionidae and Urocoptidae (both in Urocoptoidea) are most closely related to the Helicoidea, a clade represented by multiple families in our study.

## DISCUSSION

Molecular data strongly supports the inclusion of the genus *Mexistrophia* in the Cerionidae, an assignment originally based on anatomical data and shell morphology. The topology of the phylogram of the Cerionidae is concordant with the branching patterns in the zoogeographic hypothesis for the distribution of Cerionidae (Figure 1), although several geographic regions are not yet represented by molecular data.

Results of this analysis also recovered a sister group relationship between Cerionidae and the urocoptid *Microceramus pontificus*, supporting the inclusion of Cerionidae within Urocoptoidea, as advocated by Uit de Weerd (2008), and contradict its placement within Clausilioidea (Baker, 1961; Solem, 1978; Tillier, 1989). To date, Cerionidae have been included in very few of the broader molecular studies of pulmonate phylogeny. Based on ribosomal RNA sequences, Wade and co-authors (2001: fig. 1) show *Cerion* as the sister taxon to Helicoidea + Spiraxidae + Haplotremidae, but do not include Urocoptidae among their sampled taxa. Topology of the more basal portions of our tree are generally consistent with results of other molecular studies on phylogenetic relationships among Pulmonata (e.g., Wade et al., 2006; Dayrat et al. 2011; White et al. 2011) when adjusted for taxon sampling and rooting.

The phylogenetic relationships within Cerionidae suggest that the near-shore, halophilic habitat that has commonly been associated with this family is likely a Cenozoic adaptation that coincided with the transition from continental to island habitats.

As reported by Thompson (2011: 190), *Mexistrophia* species inhabit cool mesic or submesic temperate forests, at elevations greater than 2000 m and distances in excess of 200 km from the nearest coastline. *Mexistrophia* is an early offshoot of a lineage that dates back to “*Cerion*” *acherontis* from the Hell Creek Formation [Upper Cretaceous (Maastrichtian)] of northeastern Montana. This species was part of a faunule that consisted almost entirely of fresh water forms (Roth and Hartman, 1998: Table 1). The habitat for this faunule has been interpreted as a subtropical, flat, forested floodplain. Similarly, the genus *Brasilennea* (Maury, 1935), recently transferred to the Cerionidae (Salvador et al., 2011), was endemic to the Middle to Late Paleocene Itaboraí Basin of Brazil. This genus was part of a fauna that included numerous terrestrial snails and mammals. Maury (1935: 4) commented that a crocodilian jaw was associated with the fossils she described. Salvador and Simone (2012: 49) noted that little is known about the paleoenvironment of the Itaboraí Basin, other than its high calcium carbonate availability, and cited reports that this basin had a wet and warm climate with copious vegetation.

*Cerion uva* represents the most basal lineage within the Cerionidae that is limited to island habitats. This species is endemic to the islands of Aruba, Bonaire and Curaçao, and is widely distributed throughout these islands (Harasewych, 2014: fig. 4), occurring on limestone plateaus along the coast, as well as further inland, even at elevations of 200 m or more. There are few places on these hot, arid islands that are more than 5 km from the ocean. Windborne salt spray and salt particles reach most or all parts of these islands. All remaining species of Cerionidae are limited to islands ranging from southern Florida throughout the Bahamas, Cuba, Cayman Islands, Hispaniola, Puerto Rico and the western Virgin Islands, where they occur on or near living or dried terrestrial vegetation, generally at low elevations and in close proximity to the shoreline. Some populations occur at elevations of tens of meters, usually near the edges of coastal cliffs. Populations of some normally coastal species may occasionally be found several kilometers inland, generally on the windward sides of islands.

When the progenitors of *Cerion* were first isolated on small, arid islands, most likely in the early to mid-Tertiary, selection favored animals that were salt tolerant and able to withstand heat, exposure to sun, and prolonged periods of desiccation. Descendants of these animals colonized the islands of the Greater Antilles along the GAARlandia land bridge during the late Eocene-early Oligocene and later the Bahamas via a stochastic accumulation of hurricane-borne propagules (Ituarralde-Vinent, 2006: figs. 6, 13; Harasewych, 2012: 123).

Although *Cerion acherontis* Roth and Hartman, 1998, the Cretaceous ancestor of Cerionidae, was provisionally described in the genus *Cerion*, its inclusion in *Cerion* would render this genus paraphyletic due to the intervening phylogenetic positions of the genera *Mexistrophia* and *Brasilennea*. We therefore propose *Protocerion* as a new genus for this Cretaceous species.

### *Protocerion* new genus

**Type Species:** *Cerion acherontis* Roth and Hartman, 1998. (By original designation)

**Diagnosis:** Shell of moderate size (~ 23 mm), pupiform in shape, apically rounded, elongate-ovate (shell length/shell width ~ 2.7). Protoconch and early whorls unknown. Teleoconch of 4+ smooth, weakly convex whorls, with impressed suture. Sculpture of faint growth lines. Umbilicus imperforate. Aperture rounded, slightly higher than wide, ~ 3/8 of shell length. Peristome adpressed, forming thin parietal callus and thickened, axial columellar lip, smoothly rolled outward. Lacking columellar or parietal folds.

**Distribution:** Known only from a single, fractured and compressed specimen (Figure 3) collected ~ 29.8 m above the base of the Hell Creek Formation, Garfield County, Montana (106°56'47" N, 47°34'10" N). Late Cretaceous (Late Maastrichtian).



**Figure 3.** The holotype and only known specimen of *Cerion acherontis* Roth and Hartman, 1998, the type species of *Protocerion* new genus. USNM 491763, Hell Creek Formation, Garfield County, Montana [106°56'47" N, 47°34'10" W]. Late Cretaceous (Late Maastrichtian).

**Remarks:** As noted by Roth and Hartman (1998), *Protocerion acherontis* more closely resembles the smooth-shelled morphotype exemplified by the Recent species *Cerion incanum* (Leidy, 1851) than any of the ribbed morphotypes (e.g., *Cerion uva*). Both *Protocerion* and *Mexistrophia* lack columellar or axial folds, which are present in *Brasillenea* and all species of *Cerion*. These folds are an apomorphy for *Brasillenea* + *Cerion* that is lacking in *Protocerion* and *Mexistrophia*. Their absence in *Protocerion* distinguishes this genus from *Cerion*.

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# A new species of the genus *Mexipyrgus* Taylor, 1966 (Caenogastropoda: Truncatelloidea: Cochliopidae) from late Holocene spring deposits in Viesca, Coahuila, Mexico

Alexander Czaja

José Luis Estrada-Rodríguez

Ulises Romero-Méndez

Faculty of Biological Sciences

Juarez University of the State of Durango (UJED)

35010 Gómez Palacio, Durango, MEXICO

aaczaja@hotmail.com

## ABSTRACT

A new species of the genus *Mexipyrgus* Taylor, 1966 (Caenogastropoda: Truncatelloidea: Cochliopidae) is described from two Holocene springs in Viesca, Coahuila, Mexico. Previously, only one species was known in this genus, *Mexipyrgus carrrazae* Taylor, from freshwater springs and streams in the Cuatrocienegas Valley in Coahuila, Mexico. Similar to the extant species, the shells of *Mexipyrgus viescaensis* new species show a high level of morphological variability.

*Additional Keywords:* *Mexipyrgus carrrazae*, freshwater gastropod, subfossil endemic

## INTRODUCTION

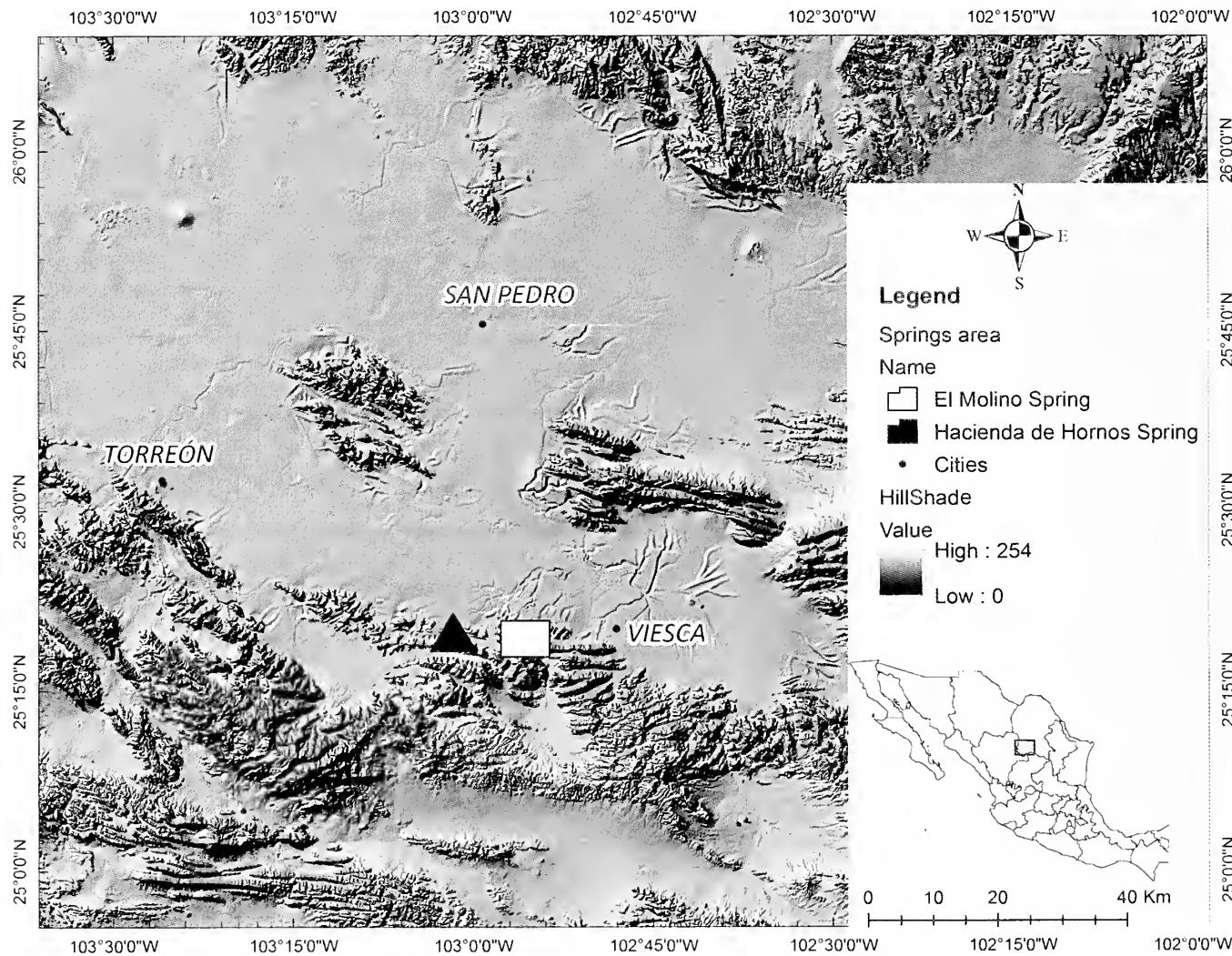
The Chihuahuan Desert in United States and Mexico is considered as a hotspot of molluscan diversity, with a high number of endemic gastropod species (Hershler, 2011). One of the most interesting sites in this desert is Cuatrocienegas Valley in Coahuila, Mexico. The relatively small valley contains more than 70 endemic species of animals and plants, and is biologically the most diverse site in North America, in relation to endemism (Stein et al., 2000). The malacologist Dwight Willard Taylor, who had presented a first monograph of the snails of Cuatrocienegas, considered the mollusks of this site as "...the most spectacularly endemic fauna of freshwater snails known in the Western Hemisphere..." (Taylor, 1966). The freshwater ecosystem of Cuatrocienegas includes five endemic genera of hydrobiid snails (*Paludiscala*, *Coahuilix*, *Mexithauma*, *Nymphophilus* and *Mexipyrgus*). Fossil records of Cuatrocienegas endemic species from other sites were reported only by Czaja et al. (2014a). The authors discovered in the Valley of Sobaco, Coahuila, a system of paleo-lakes with a malacofauna similar to the modern snail communities of Cuatrocienegas. This includes the endemic genus *Coahuilix*.

*Mexipyrgus* is a Mexican endemic freshwater hydrobiid gastropod that lives in springs, lakes, and the Mezquites River in the Valley of Cuatrocienegas. Its main morphological characteristic is a thickened, strongly sculptured shell with color banding. All these shell features are unusual for freshwater snails, especially within the family Cochliopidae. Geographic variation in shell morphometry of *Mexipyrgus* was analyzed by Hershler and Hayek (1988). Aspects of ecology and coevolution between *Mexipyrgus carrrazae* and its fish predator, *Herichthys minckleyi*, have been subject of various investigations (Smith, 1982; Tang and Roopnarine, 2003; Johnson et al., 2007; Covich 2010; Chaves-Campos et al., 2012).

In sediments of two recently dried-up springs near the town Viesca, Coahuila, specimens of a second species of the genus *Mexipyrgus* Taylor were collected (Figure 1). The springs are located at the foot of the *Sierra la Cadena* and belong to a system of several water bodies that have provided water to small settlements at the vicinity. Both sites contain an abundance of shells including several possibly new species of *Tryonia*, *Pyrgulopsis* and *Pyrgophorus* (Czaja, personal data). Similar to *Mexipyrgus carrrazae* from Cuatrocienegas, the shells from Viesca possess a high level of phenotypic variability. The aim of the present study is to describe the new species of *Mexipyrgus* and to show its similarities and differences to the living species from Cuatrocienegas.

## MATERIALS AND METHODS

Specimens of *Mexipyrgus viescaensis* new species were collected from two recently dried-up springs near the town Viesca, Coahuila, Mexico, approximately 2 km south of the locality Venustiano Carranza (spring El Molino: 25°19'55" N, 102°55'49" W; spring Hacienda de Hornos y Carranza: 25°20'05" N, 102°57'39" W). The material derives from outcrops on the edges of the springs. The



**Figure 1.** Map of the study area with localization of the springs of Viesca.

section is approximately 1.5 m thick and contains unconsolidated sediments, small travertine pieces and shell debris. The sub-recent (late Holocene) age of the superficial deposits is confirmed by several reports and photographs which document the desiccation of the springs during the drought of 1958/59.

The sediments of both sites were screened through 0.5 mm and 0.3 mm sieves. The shells were photographed with a Zeiss AxioCam ERc5s microscope-camera. The shells of the new species were compared directly with *Mexipyrgus carrrazae* from the Malacological Collection of the Faculty of Biological Sciences, Juarez State University of Durango. All collected material is housed at the same Faculty.

## SYSTEMATICS

Class Gastropoda Cuvier, 1795  
 Subclass Caenogastropoda Cox, 1960  
 Superfamily Truncatelloidea Gray, 1840  
 Family Cochliopidae Tryon, 1866

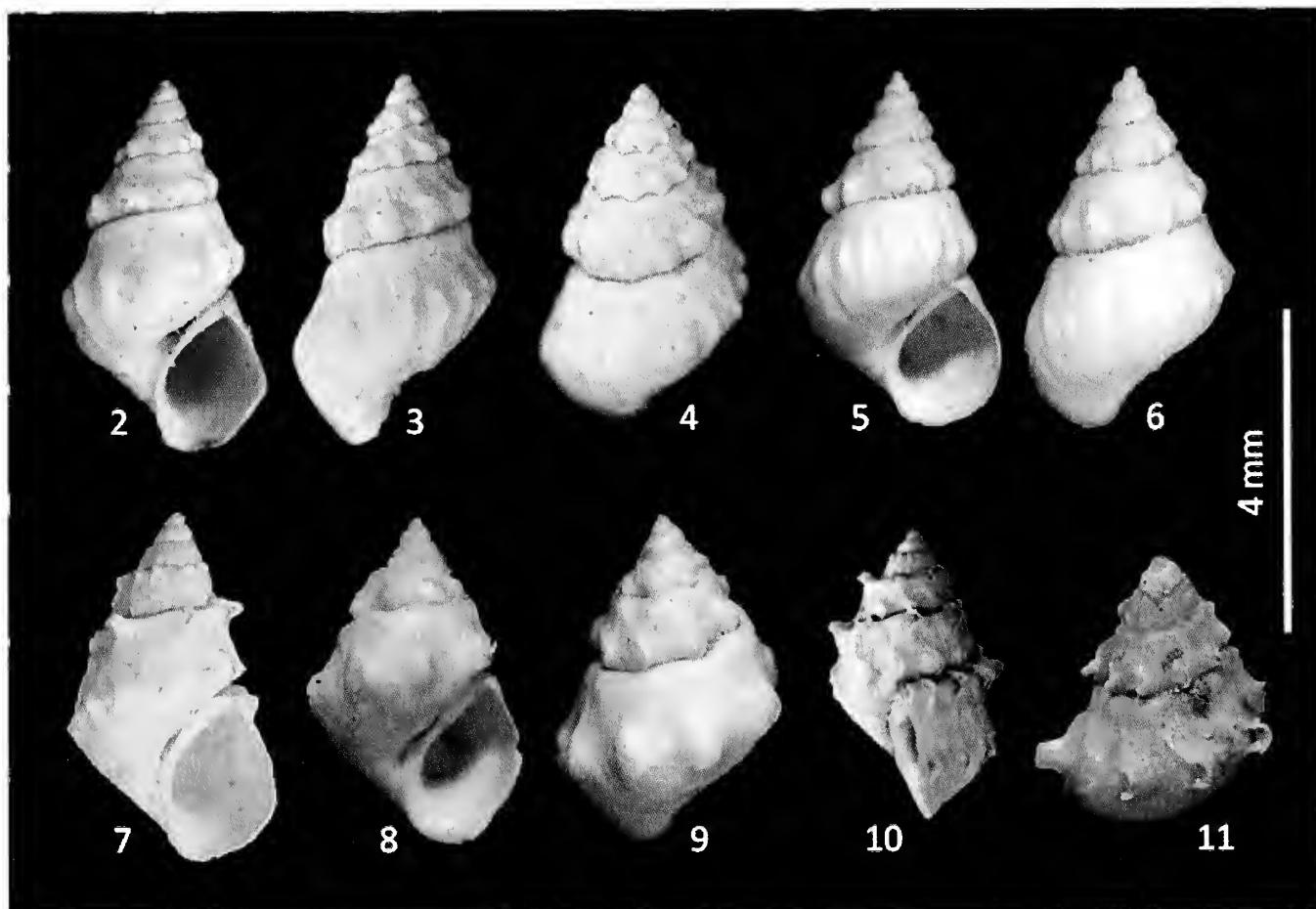
### Genus *Mexipyrgus* Taylor, 1966

**Type Species:** *Mexipyrgus carrrazae* Taylor, 1966 (by original designation).

#### *Mexipyrgus viescaensis* new species (Figures 2–11)

**Diagnosis:** Shell medium-sized, thick, white to beige colored, conical to turriform, height 3.18–4.90mm, width 1.99–2.45mm (shell measurements in Table 1), with 5.25 to 6.25 whorls, whorls flattened, aperture elongate-ovate, outer lip prosocyt, inner lip not adnate to parietal wall, sculpture with strong spiral and axial elements, with prominent knobbed ribs or spines, sculpture variable.

**Description:** Shell medium-sized, thickened, conical to turriform, with 5.00–6.25 whorls. Whorls flattened with sutures not very impressed; lower whorls develop a prominent spiral swelling anterior to suture (subsutural cord). Height 3.18–4.90 mm, width 1.99–2.45 mm. Aperture elongate-ovate, somewhat pyriform, angulate



**Figures 2–11.** *Mexipyrgus viescaensis* new species. **2–4.** Holotype, UJMC-200. **5–6.** Paratype 1, UJMC-201. **7.** Specimen showing spines, UJMC-202. **8–9.** Paratype 2, UJMC-203. **10–11.** Specimens with shovel-shaped spines. **10.** UJMC-204. **11.** UJMC-205.

above; inner lip not adnate to parietal wall forming a narrow gap between lip and pariental wall; outer lip strongly prosocyr; aperture 1.90 mm height and 1.25 mm wide (holotype). Protoconch and second whorl smooth. Sculpture with spiral and axial elements beginning at third whorl; spiral cords close to suture; wave-like axial ribs developing on third whorl, with prominent knobs where they cross spiral cords; knobs at lower part of whorls prominent, sometimes with shovel-shaped spines emerging from sub-sutural knobs; after third whorl knobbed ribs very prominent; sculpture reduced on last part of body whorl. Axial growth lines prosocyr to sinusoidal, prominent. Color beige or white, original coloring (periostracal color bands?) and operculum not preserved.

**Type Material:** Holotype (Figures 1–3, 15), UJMC-200, 4.15 mm height, 2.05 mm width, 6.25 whorls. Paratype 1 (Figures 5, 6), UJMC-201, 4.22 mm height, 2.39 mm width, 6.00 whorls. Paratype 2 (Figures 8, 9), UJMC-203, 4.09 mm height, 2.50 mm width, 5.25 whorls. Alexander Czaja and José Luis Estrada-Rodríguez coll., 2014. All from type locality.

**Type Locality:** Spring *Hacienda de Hornos y Carranza*, ca. 15 km west of the town Viesca, Coahuila, Mexico (25°20'05" N, 102°57'39" W).

**Stratum Typicum:** Holocene (sub-recent).

**Other Material Examined:** More than 500 specimens from the type locality and 215 specimens from spring *El Molino*.

**Etymology:** The new species is named after Viesca, Coahuila, a small town near the dried springs.

**Geographic Distribution:** Endemic to the springs *Hacienda de Hornos y Carranza* and *El Molino* near Viesca, Coahuila, Mexico.

**Remarks:** The new species differs from other members of the family Cochliopidae by their strongly thickened and highly sculptured shells with spiral cords and knobbed ribs, which allocate the species into the genus *Mexipyrgus*. Some species of the genera *Tryonia*, *Pyrgophorus*, and *Lithococcus* also have sculptured shells but differ by the following characters: species of the first

Table 1. Measurements and basic statistics of length and width of shells of *Mexipyrgus viescaensis* new species.  $\bar{x}$  = mean,  $\sigma_x$  = standard deviation, N = sample size.

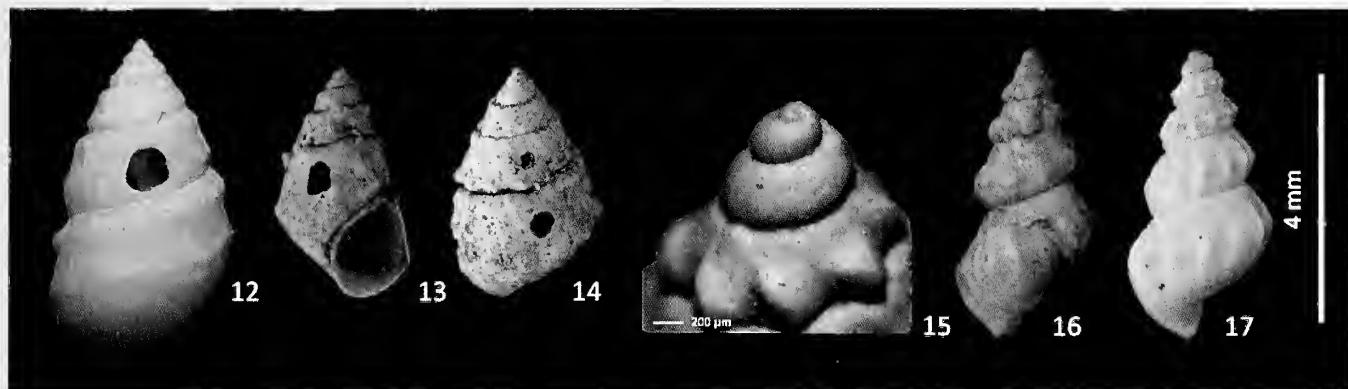
Specimen	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	$\bar{x}$	$\sigma_x$	N
Length (in mm)	3.51	4.09	3.62	3.42	3.71	3.63	4.01	3.81	3.43	4.12	4	3.91	3.72	3.18	3.82	3.41	3.42	3.92	4.22	3.67	3.73	3.72	20
Width (in mm)	2.01	2.5	2.38	2.01	2.42	2.11	2.45	2.13	1.99	2.21	2.51	2.22	2.19	2.03	2.24	2.39	2.01	2.12	2.39	2.29	2.23	0.177	20
No. whorls	5.25	5.25	5.25	5.25	5.25	5.50	5.50	5.25	6.00	5.00	5.25	5.00	5.25	5.25	5.25	5.25	5.25	5.25	6.25	6.00	5.41	0.356	20

two genera do not have knobbed ribs and the shells of *Lithococcus* are globose-trochoid.

Considerable variation of shell features occurs among the populations of both sites where the species was found. Variation showing ribs with reduced knobs is shown on Figure 13. That morphotype possesses two spiral cords with knobbed ribs close to the sutures. The number of knobbed ribs on the whorls varies between 8 and more than 20 (Figures 5, 6, and 8) and, in particular, specimens from *Hacienda de Hornos y Carranza* Spring have shells with numerous fine ribs (Figures 5 and 6). Figures 7, 10, and 11 show another variation with prolonged spines on the spiral cords. In some specimens from the *El Molino* Spring these shovel-shaped spines on the knobs are sometimes connected between the sutures (Figure 10). This phenotype is the least similar to the holotype and shells with this kind of sculpture are smaller, reaching just 3.5 cm in length. Intergradation occurs among the morphotypes from the same springs but most shells closely resemble the holotype.

Originally six nominal species of *Mexipyrgus* were described by Taylor (1966), based on characters like shell size, shell sculpture and periostracal bands. But Hershler (1985) could prove that all specimens of *Mexipyrgus* from Cuatrocienegas belong to a single variable species and that the differences in the shell features are dependent on environmental factors. According to Vermeij and Covich (1978) and Covich (2010) *Mexipyrgus* and other snails from Cuatrocienegas evolved in coevolution with snail-eating cichlid fishes. Also the sub-recent material of both springs of Viesca show a high level of phenotypic variability among the populations in time and space. We find in the same horizons with specimens of *Mexipyrgus* pharyngeal teeth of fishes (probably cichlids). Approximately 10% of all shells in the springs were perforated (Figures 13–14). Similar holes in shells were described recently by Rasser and Covich (2014) from Miocene Lake Steinheim, Germany, and interpreted as perforations of a fish predator. We suppose that the thickened and strongly sculptured shells of *Mexipyrgus* of both springs could be a direct adaptive response to strong fish predation. Further studies on shells of the new *Mexipyrgus* from Viesca will show more details of the predator-prey interaction during the coevolution of these species.

*Mexipyrgus viescaensis* is clearly distinguished from *Mexipyrgus carranzae* mainly by its size and by the sculpture of the shells. While shells of *M. carranzae* attain a length up to 8.45mm (Hershler, 1985, p. 99), the largest specimens from Viesca reach just 4.85mm. Shells of *Mexipyrgus carranzae* are thicker (more than 0.25mm thickness) than specimens from Viesca (less than 0.20mm thickness). Most diverse and stronger is the sculpture of shells of *M. viescaensis* with very prominent and strong knobs on the spiral cords and shovel-shaped spines. Spines on whorls have never been observed on living snails from Cuatrocienegas. Another difference is that by *M. viescaensis* the inner lip are not adnate to the parietal wall forming a narrow gap between the lip and parietal wall. Shells of *M. carranzae* lack this gap.



**Figures 12–17.** *Mexipyrgus viescaensis* new species, *Mexipyrgus carrranzae* Taylor, from Poza Becerra, Cuatrocienegas Valley, Coahuila, Mexico, and *Tryonia hershleri* Czaja and Estrada-Rodríguez from Paleolake Irritila, Coahuila, Mexico. **12.** *Mexipyrgus carrranzae* Taylor, hole on the ab-apertural side on the shell. **13.** *Mexipyrgus viescaensis* new species, hole on the apertural side on the shell. **14.** *Mexipyrgus viescaensis* new species, double holes on the ab-apertural side on the shell. **15.** *Mexipyrgus viescaensis* new species, Holotype (UJMC-200), protoeonch view. **16.** *Mexipyrgus viescaensis* new species from Viesca, Coahuila. **17.** *Tryonia hershleri* Czaja and Estrada-Rodríguez from Pleistocene Paleolake Irritila, Coahuila, Mexico.

The findings of a new species of *Mexipyrgus* shed new light on the origin of the endemic *M. carrranzae* from Cuatrocienegas. Of the five endemic genera from Cuatrocienegas Valley, four, *Coahuilix*, *Paludiscala*, *Nymphophilus*, and *Mexipyrgus*, have already been found as (sub-) fossils outside the basin (Hershler, 1985; Czaja et al., 2014a; Czaja, personal data). *Mexipyrgus* is possibly a relict genus which originally had a wider distribution with different species. Interestingly, some morphotypes of *M. viescaensis* show great similarity with shells of *Tryonia hershleri* (Figures 16–17). This species with thickened and strong sculptured shells was newly reported from Late Pleistocene deposits near Viesca (Czaja and Estrada-Rodríguez, 2015). This similarity may be due to convergence but on the other hand, there are also molecular evidences that both genera are closely related (Hershler et al., 1999; Hershler et al., 2005). This might be proved only by fossil findings in Cuatrocienegas Valley and Viesca. Future work on sub-fossil shells in both localities will allow us to know more on the evolutionary path of the enigmatic genus *Mexipyrgus* from northern Mexico.

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# Intracapsular development in the freshwater gastropod *Chilina dombeiana* (Bruguière, 1789) (Gastropoda: Hygrophila: Chilinidae)

Jéssica Bórquez

Departamento de Ecología  
Facultad de Ciencias  
Universidad Católica de la Ssma.  
Concepción, CHILE

Claudio Valdovinos

Departamento de Sistemas Acuáticos  
Facultad de Ciencias Ambientales y  
Centro de Ciencias Ambientales (EULA)  
Universidad de Concepción, CHILE

Antonio Brante<sup>1</sup>

Departamento de Ecología  
Facultad de Ciencias y  
Centro de Investigación en Biodiversidad  
y Ambientes Sustentables (CIBAS)  
Universidad Católica de la Ssma.  
Concepción, CHILE  
abrante@ucsc.cl

## ABSTRACT

*Chilina dombeiana* (Bruguière, 1789) is a native Chilean species inhabiting freshwater and estuarine environments. In the present study, a series of stages for embryonic development of the embryo is described. The snails lay gelatinous and transparent zig-zag-like string egg masses, ranging between 10 and 130 mm in length. Each egg mass contains a variable number of embryos ranging from 60 to 298 eggs with a mean density of  $2.9 \cdot \text{mm}^{-2}$  ( $\pm 0.7 \text{ SD}$ ). Embryos inside egg masses are individually encapsulated and embedded in a jelly matrix. Hatching as crawling juveniles took place after 28 days, indicating that direct development occurs in this species. In contrast to other freshwater pulmonates, the well-developed operculum observed in *C. dombeiana* from the veliger stage, suggest a marine ancestry for this species.

**Additional Keywords:** Chilinidae, Bio-Bío river, hermaphroditism

## INTRODUCTION

Chilinidae is an ancient family of freshwater gastropods endemic to South America (Jáne et al., 2010). The family is monotypic, with *Chilina* including the primitive pulmonate snails described by Gray in 1828 (Brace, 1983). *Chilina dombeiana* (Burguière, 1789) is a native Chilean species that inhabits freshwater and estuarine environments from approximately 35° S to 37° S (Valdovinos, 2006). Although this species is highly abundant in some rivers and lakes, and may play an important ecological role in freshwater ecosystems (Valdovinos et al. 2006), there is little information about the basic biology of this organism.

Species of the order Hygrophila shows simultaneous hermaphroditism and are capable of self-fertilization and/or biparentality through cross-fertilization (Jáne et al., 2010; Nakadera et al., 2014). However, there is no published information on the reproductive behavior and embryonic

development of *C. dombeiana*. We describe herein the intracapsular development of individuals of *C. dombeiana* inhabiting a riverine environment in south-central Chile.

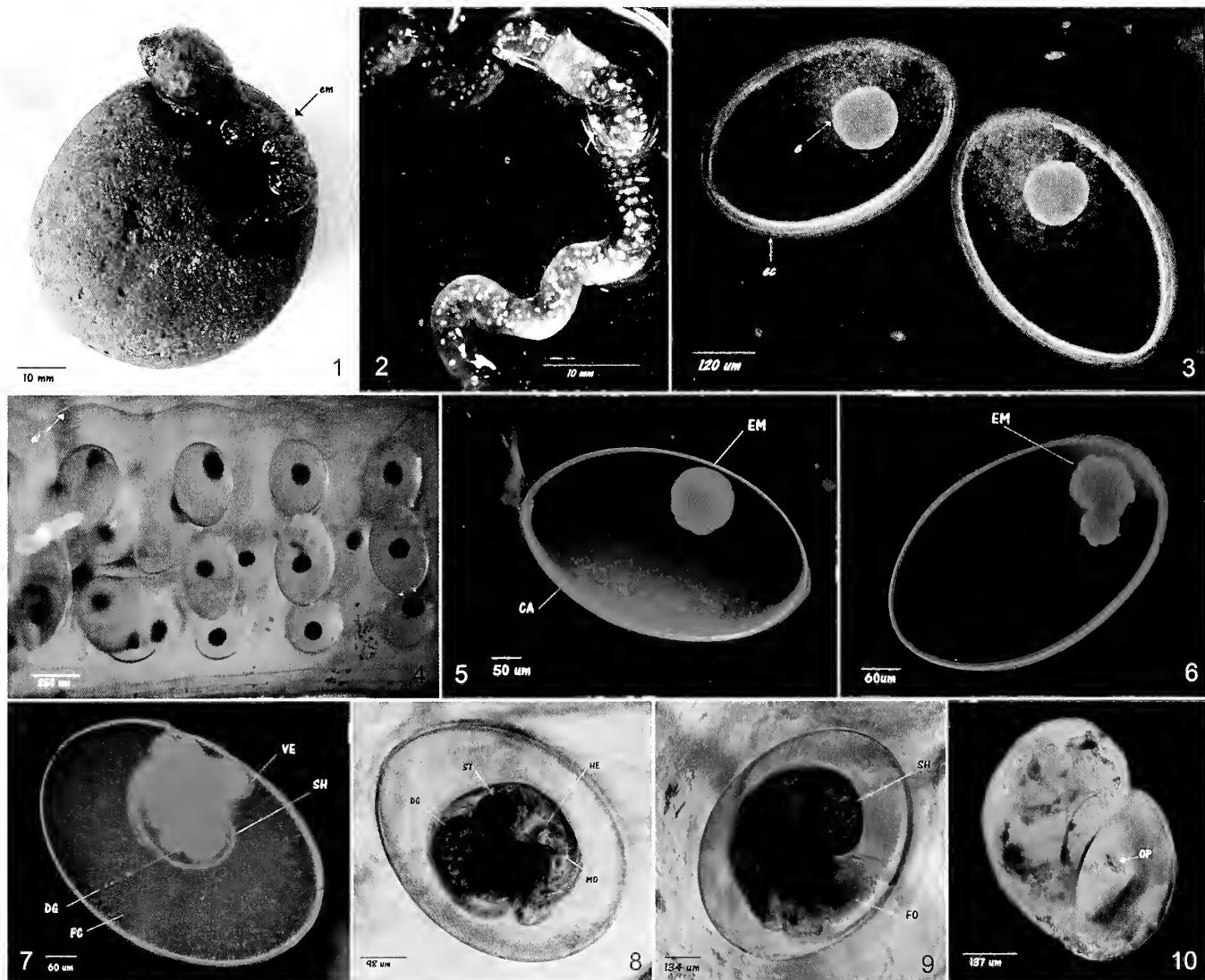
## MATERIALS AND METHODS

At one site in the Bio-Bío river (36°49'22.43" S, 73°6'31.41" W) in Concepción, Chile, 50 individuals of *C. dombeiana* were collected by hand and transported to the Facultad de Ciencias, Universidad Católica de la Ssma. Concepción. In the laboratory, the *C. dombeiana* adults were cultivated in individual plastic boxes (200 ml) filled with freshwater collected from the sample site. Boxes were constantly aerated with an air pump and the temperature was maintained at 18°C. The water inside the boxes was changed every ten days. Once the individuals had laid egg capsules, the relative duration of each developmental stage (in days), a range of total number of egg by egg mass, egg and embryo size, and embryonic development traits were recorded. In order to make these measurements, 20 egg masses from different individuals were haphazardly chosen and photographed every three days under a microscope (10×; Olympus CX31) connected to a tablet computer equipped with a digital camera (Smart Pad 500). Five stages of embryonic development were observed: early embryo, trophophore, early veliger, late veliger, and pre-hatching juvenile. Embryo size was measured with the software Image measure (VMS3.5). In addition, when the egg mass showed a string formation (Figures 1, 2), the total number of embryos per clutch was estimated by counting the number of embryos in a section of the egg mass and extrapolating to the total egg mass size. This was done using a binocular microscope (0.67×; Olympus CX31).

## RESULTS AND DISCUSSION

Sexual maturity of the freshwater snail *C. dombeiana* is reached within the first year of the individual's life cycle

<sup>1</sup> Corresponding Author



**Figures 1–10.** *Chilina domebeiana*, egg capsules and intracapsular development. **1–4.** Egg capsules. **1.** Gelatinous egg mass (em) attached to hard substrate. **2.** Egg mass showing the general zig-zag string appearance. **3.** Light micrograph showing the embryos (e) contained within each egg capsule (ec). **4.** Detail of the external layer (el) of the egg mass surrounding the egg capsules. **5–10.** Intracapsular development. **5.** Segmented egg. CA: egg capsule; EM: embryo. **6.** Trochophore stage. EM: embryo. **7.** Early veliger stage. DG: digestive gland; FC: intracapsular fluid; SH: shell; VE: velum. **8.** Veliger stage. DG: digestive gland; HE: heart; MO: eyespot; ST: stomach. **9.** Late veliger stage. FO: foot; SH: shell. **10.** Pre-hatching juvenile. OP: operculum.

(C. Valdovinos; unpublished data). In our observations, the smallest individual laying egg masses was 11.7 mm in shell size. Individuals lay gelatinous and transparent egg masses on rocks.

The egg masses had a zig-zag-like string formation ranging between 10 and 130 mm in length (Figures 1, 2). Within each egg mass, embryos were observed individually encapsulated and embedded within a gelatinous matrix (Figures 3, 4). The total number of embryos per egg mass ranged from 60 to 298 with a mean density of  $2.9 \text{ eggs} \cdot \text{mm}^{-2}$  ( $\pm 0.7 \text{ SD}$ ). In the first 4 days of development, the early embryos were characterized by cleaved eggs and embryos at the pre-trochophore stage with an average size of 120.9  $\mu\text{m}$  ( $\pm 11.8 \text{ SD}$ ; Figure 5; Table 1).

The embryos were yellow in color and were embedded in a transparent intracapsular fluid. No apparent major movement of the embryos was noticed. Between days 5 and 6 of cultivation, the embryos developed into early and late trocophores had a mean average diameter of 139.4  $\mu\text{m}$  ( $\pm 11.1 \text{ SD}$ ; Figure 6; Table 1). Between days 12 and 15, early veliger embryos with velum and noticeable development of a very soft shell (average size of 235.5  $\mu\text{m}$   $\pm 8.1 \text{ SD}$ ; Table 1) at the apical end were observed (Figure 7). In addition, at this stage, digestive gland and active movement of the larvae inside the capsules were visible. After 16–19 days of development, the intracapsular fluid became more transparent. Embryo at this late veliger stage had a well-developed velum with an average shell size of

**Table 1.** Developmental time (days) and average size ( $\mu\text{m}$ ) of embryos of the freshwater gastropod *Chilina dombeiana* at different developmental stages. Thirty embryos were measured at each stage (excepting stage 2 were only 10 embryos were recorded).

Stage	Traits	Mean Size ( $\mu\text{m}$ ) $\pm$ SD	Time (days)
1	Egg fertilized with subsequent first cleavages, blastula to gastrula stage.	120.9 $\pm$ 11.8	3–4
2	Troehophore stage progresses becomes to have an elongated shape of embryos	139.4 $\pm$ 11.1	1–2
3	Pre-veliger embryos stage displayed movement with noticeable development of very soft shells at the apical end and digestive gland.	235.5 $\pm$ 8.1	4–5
4	Veliger embryo stage with the spiralization process of the shell, appearance of two eye spots, heart activity and transparent operculum. Increase calcification of the shell and the development of the digestive gland.	394.5 $\pm$ 12.5	10–12
5	Pre-hatching veliger characterized by a hard and dark brown shell, foot and operculum fully developed, and most morphological traits like adults. High mobility of individuals.	505.6 $\pm$ 11.4	5–7

394.5  $\mu\text{m}$  ( $\pm$  12.5 SD) (Figures 8, 9; Table 1). In addition, coiling of the calcified shell, the dark pigmented eyespots, the transparent operculum, and the digestive gland were also evident. At this stage, the embryo had a high heart rate. Between days 23–29, pre-hatching juveniles were observed inside capsules. The shells were well calcified and had a reduced velum (Figure 10). The foot muscle and operculum were fully developed and individuals actively moved inside the capsule. At this stage, the mean shell size was 505.6  $\mu\text{m}$  ( $\pm$  11.4) (Table 1). Hatching as crawling juveniles took place after 28 days, indicating that direct development occurs in this species.

Adult freshwater pulmonates usually lack an operculum, the exception being the family Amphibolidae (see Golding, Ponder, and Byrne, 2007). *Chilina dombeiana* differs completely from other non-amphibolid freshwater pulmonates by having a well-developed operculum. This suggests that *C. dombeiana* could have an evolutionary origin from marine ancestry. Phylogenetic studies on this group would shed light on the evolution of this species and the potential adaptation of populations of these snails to freshwater habitats (see Harry, 1964; Barker, 2001).

Although the range of *C. dombeiana* is restricted latitudinally from 35° to 37° S (Valdovinos, 2006), this species can be found abundantly at estuarine river mouths all the way to upper river basins characterized by well-oxygenated, clean, and cold water. As has been suggested for other gastropod species (e.g., Pechenik, 1983; 1986; Rawlings, 1996; Pande et al., 2010), the direct and encapsulated development of *C. dombeiana* would allow this organism to tolerate extreme environmental conditions during its entire embryonic phase. Although direct development may lead to restricted dispersal of this species, potentially dislodged egg masses or capsules from the substrata would favor population connectivity and gene flow via river currents. Considering that human use of freshwater ecosystems causes the greatest negative impact on these ecosystems (Strayer and Dudgeon, 2010), large anthropogenic perturbations could expose freshwater invertebrates to specific threats that may result in local extinction processes. Accordingly, Valdovinos (2006) highlighted the vulnerability of the Chilinidae family due to significant habitat lost. In that study, the author further emphasized the importance of conducting more

studies that contribute to the understanding of these freshwater gastropods.

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# *Trophon geversianus* (Pallas, 1774): the first record of communal egg masses in the muricid subfamily Trophoninae (Gastropoda)

**María José Pio**  
**Guido Pastorino**

Museo Argentino de Ciencias Naturales,  
Av. Ángel Gallardo 470 3º piso, Lab. 57  
C1405DJR Buenos Aires, ARGENTINA  
mjpio@macn.gov.ar  
gpastorino@macn.gov.ar

**Gregory S. Herbert**

School of Geosciences  
University of South Florida  
4202 E. Fowler Avenue  
Tampa, FL 33620 USA  
gherbert@usf.edu

## ABSTRACT

Reproductive strategies are thought to have played a major role in the adaptive radiation of neogastropods, but data are still lacking for important taxa, and the extent of plasticity in reproductive strategies is not well understood. Females of the Patagonian neogastropod *Trophon geversianus* are here shown for the first time to have plastic egg capsule-laying strategies. Past work has recorded only egg laying by isolated females, both in the intertidal and in the lab. New observations of egg laying in subtidal *T. geversianus* show that communal oviposition also occurs in this species, a first record of its kind for the species and for the subfamily Trophoninae. Given that communal oviposition in other species is commonly regarded as an adaptation to predation cues or changing environment, we propose this reproductive strategy in trophonines is an inducible response to environmental risk.

## INTRODUCTION

In the course of gastropod evolution, many species have evolved reproductive adaptations related to the encapsulation of embryos in response to diverse environmental threats, such as predation (Rawling, 1994). Selective pressures such as predation can affect gastropod embryonic development, capsule morphology, and also oviposition behaviors, including effects that are phenotypically inducible responses (among others: Harasewych, 1990; Rawlings, 1990; 1994; Dumont et al., 2008; Bigatti et al., 2010; Roche et al., 2011).

Communal oviposition, which has evolved independently in many animal groups, consists of several conspecific females depositing egg capsules on a shared substrate, often resulting in large masses of eggs (D'Asaro, 1970; D'Asaro, 1991; Swanson, 2004). Adaptive explanations for this behavior include predator deterrence for embryos and facilitation of social foraging (Waldman, 1982; Dumont et al., 2008). Communal oviposition is a phylogenetically widespread behavior in gastropods (Thorson, 1940;

Giglioli, 1955; Gohar, and Eisawy, 1967; D'Asaro 1970; Bandel 1975; Soliman, 1987; D'Asaro, 1991) and is particularly well documented in the neogastropod family Muricidae, including the subfamilies Muricinae, Ocenebrinae and Rapaninae.

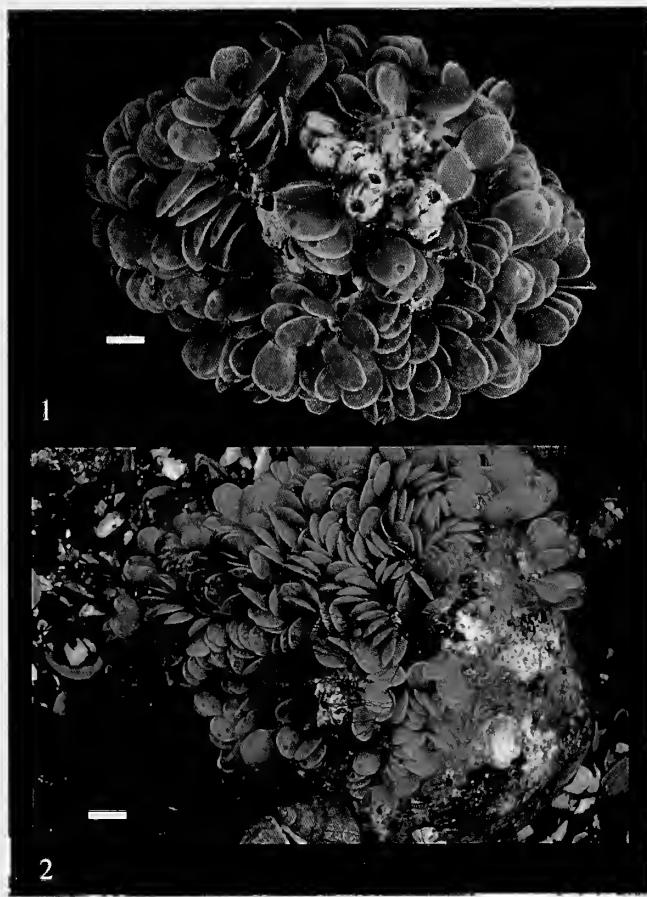
*Trophon geversianus* (Pallas 1774), type species of the type genus of the subfamily Trophoninae and a good representative taxon of the Magellanic malacological province, occurs, lives, and feeds, on banks of mytilid bivalves and barnacles on the rocky intertidal and subtidal zones along the Patagonian coast (Pastorino, 2005). Its egg capsules are easily identifiable in the field due to their abundance and characteristic erect, rounded form and bright yellow color. Capsules are variable in size (up to 22 mm in height) and are usually attached by the female to a hard substratum by a short and wide peduncle that rises from a common basal membrane (Zaixso, 1973; Penchaszadeh, 1976). Observations on the number of capsules from a single oviposition event range from 2 to 22 per female (Penchaszadeh, 1976). Cumplido et al. (2010) published observations on the spawning behaviour of *T. geversianus* in lab aquaria and reported no events of communal spawning. Communal oviposition has also not been reported previously for *T. geversianus* in the wild.

## MATERIALS AND METHODS

In this work, we report observations on communal spawning of *T. geversianus* found living at approximately 20 m depth on a mixed bottom of thick sand and pebbles near to Puerto Almanza at Beagle Channel (54°53'10.56" S, 67°42'6.55" W), Tierra del Fuego, Argentina on March 2010. One communal spawn mass, which was attached on a sub-square rock about 20 cm in width, was collected by SCUBA and fixed with 5% formalin in seawater (Figure 1).

## RESULTS

Several communal spawn masses were observed deposited on rocks partially covered by barnacles. One of the



**Figures 1, 2.** *Trophon geversianus* egg masses from Tierra del Fuego, Argentina. **1.** Subtidal communal spawn, fixed in 5% formalin in seawater. **2.** View of a subtidal communal oviposition *in situ*.

largest masses consisted of a total of 250 capsules. Each capsule had the escape aperture (mucoid plug) oriented toward the upper exterior of the spawn mass and was attached to the substrate by its own basal membrane. The basal membrane of a capsule was never superimposed over the basal membranes of adjacent capsules. A minimum of twelve females would have been required to form a mass of 250 capsules, assuming each female produced the maximum number of capsules recorded for a single female *T. geversianus* at a single oviposition event (Zaiko, 1973; Penchaszadeh, 1976; D'Asaro, 1991; Cumplido et al. 2010) (Figure 2).

## DISCUSSION

This study provides new information about the reproductive strategy of *T. geversianus*, which can be coded for phylogenetic analyses or used to map the evolution of reproductive strategies across Muricidae. Moreover, communal spawn masses of this type have not been observed previously at the intertidal and subtidal levels where *T. geversianus* usually occurs, indicating that females

may modify their oviposition habit in response to environmental cues.

The area where these egg capsules were collected is not exposed, is relatively quiet, and moderately shallow. No strong waves or active winds affect the coast at Puerto Almanza, which is very different from the typical intertidal conditions of the rocky shores along the Patagonian coast. Also, the substrate is a mix of free boulders, fine-grained sand, and large and immobile rocks. In this habitat, large rocks are the only suitable substrate on which to attach the capsules. This difference in environmental conditions in between intertidal and subtidal areas may explain the occurrence of communal spawning. The conditions are also favourable for gastropod predators, and it would be valuable to test whether the unusual spawning behaviour for *T. geversianus* influences reproductive success of adults.

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## Research Note

### Determining the date of publication for *Contradens* Haas and *Uniandra* Haas (Bivalvia: Unionidae)

Establishing the date of publication for a genus or species name can be a case for Sherlock Holmes, especially if the work was published in several sections over time. The dates of publication of the *Systematisches Conchylien-Cabinet von Martini und Chemnitz* are confusing, but dates of publication for Haas's (1910–1920) volume in this set have been presented by Haas (1923: 203) listed by *lieferung*, signatures (*Bogen*) in each *lieferung*, page numbers, and the year published. These data were summarized and repeated by Smith and England (1937), Johnson (1968), Welter-Schultes (1999: 190) and Coan and Kabat (2015). However, these authors used the dates of the *Lieferung* printed on the cover and not the dates printed on each signature. Solem (1967: 80) examined the copy of *Die Unioniden* available in Chicago and reported dates listed on the first page of each of the 43 signatures that make up the complete volume, but combined some of the signatures into a single citation. The copy of *Die Unioniden* in the Library of the Academy of Natural Sciences of Drexel University of Philadelphia was examined for the dates of publication found on the first page of each of the 43 signatures, combined into 13 *Heft*, or numbered parts, and *lieferung*. Each *Heft/lieferung* was published with a separate title page and year of publication and each contained 2 or more signatures and plates (Table 1). Dates of publication on the title page match the dates of the included signatures for all but three of the *heft* (47, 51, and 52), the date on the title page does not correspond to dates on the signatures (Table 1). The back cover of each *Heft/lieferung* listed the plates and figures contained and the signature numbers included in the *Heft*.

There is confusion around the original date of publication of the generic names *Contradens* Haas and *Uniandra* Haas. Many authors have used different dates for the description for both genera. The following chresonymy summarizes the various dates used for both *Contradens* and *Uniandra*:

***Contradens*** Haas, 1911: Graf and Cummings, 2015 [4 September, 2015].

***Contradens*** Haas, 1912: Simpson 1914: 1005; Van Benthem-Jutting, 1953: 33.

***Contradens*** Haas, 1913: Ortmann, 1917:107; Thiele, 1935: 821; Neave 1939: 825; Modell, 1942: 189; Stansbery and Soehngen, 1964: 17; Solem 1967: 109; Haas 1969a: 96; Haas 1969b: N420; Starobogatov, 1970: 64; Brandt, 1974: 289; Vokes, 1980:73; Vaught, 1989: 122; Millard, 2003: 1120; Graf and Cummings, 2006: 393; Graf and Cummings, 2007: 310; Bouchet and Rocroi, 2010: 30;

AnimalBase, 2015; Graf and Cummings, 2015 [12 May 2015]; ITIS, 2015 [11 September 2015]; GBIF, 2015 [11 September 2015].

***Uniandra*** Haas, 1912: Neave, 1940: 612; Haas, 1969a: 73; Haas, 1969b: N423; Brandt, 1974: 289; Vokes, 1980: 78; Vaught, 1989: 122; Millard, 2003: 1124; GBIF, 2015 [11 September 2015].

***Uniandra*** Haas, 1913: Solem, 1967: 132; Starobogatov, 1970: 64; Graf and Cummings, 2015 [12 May, 2015; 4 September 2015]; ITIS, 2015 [11 September 2015]; FADA, 2015 [11 September 2015].

Modell (1942:189) recognized the genus *Contradens* Haas, 1913 and erected the new subfamily Contradentinae Modell, 1942. Confusion was further compounded by Brandt (1974: 289) as to the priority of the two names and the type species of *Uniandra*. Brandt used *Uniandra* Haas, 1912 and included *Contradens* Haas, 1913 as a junior synonym, incorrectly listing the type species of *Uniandra* as *Unio contradens* Lea, 1838. However, neither genus was listed in the online searchable version of Neave (2015: 14 May 2015).

Graf and Cummings (2015: 12 May 2015) use *Contradens* Haas, 1913, noting Haas (1911: pl. 18) as a *nomen nudum*, referring to the description by Haas, 1913 in Conchylien Cabinet (page 173), but take the date of publication from Haas (1913). They subsequently changed the date of *Contradens* to Haas, 1911 in the version on the web with no explanation (4 Sept 2015).

The generic name *Contradens* Haas first appears in plate captions for plates 18–22 in Conchylien Cabinet (Haas, 1910–1920). Plates 18–23 and pages 81–88 were published on 1 July 1911 (Table 1). There are no dates on any of the plates, so they take the latest date of publication of the last signature in *Heft* 44 (Table 1). The generic name *Contradens* was associated with 15 previously published species and subspecies names. The generic name *Contradens* was thus available from the date of publication of the plates. This is considered an indication for a genus named before 1931 under ICZN Code articles 12.1, 12.2. The plates do not have a date on them but are included in *Heft* 44 and the last signature in this *heft* has a date of 1 July 1911.

Additionally, *Heft* 44 was stamped on the cover as received by the Library at the Academy of Natural Sciences of Philadelphia as received 16 October 1911. The plates could not have been published after the date stamped received in Philadelphia.

*Contradens* was fully described and *Unio contradens* Lea, 1838 subsequently designated as the type species by Haas (1913a: 35–36). Date of publication of this article was listed as 27 January, 1913 (Solem, 1967: 83). Haas

**Table 1.** Dates of publication of Haas (1910–1920) *Die Unioniden* based on dates on first page of 43 signatures of the copy in the Academy of Natural Sciences of Drexel University, Philadelphia.

Heft	Lieferung/Date	signature	Pages	Figures/plates	Date
41	545 [1910]	1	1–8	Pls. 1–6	1 August 1910
		2	9–16		6 August 1910
42	546 [1910]	3	17–24	Pls. 7–12	8 August 1910
		4	25–32		10 March 1910
43	549 [1911]	5	33–40	Fig. 1 Pls 12a, 13–17	13 August 1910
		6	41–48		15 August 1910
44	551 [1911]	7	49–56	Pls. 18–23	10 March 1911
		8	57–64		13 March 1911
45	554 [1911]	9	65–72	Pls. 24–29	15 May 1910
		10	73–80		30 May 1911
46	559 [1912]	11	81–88	Pls. 30–35	1 July 1911
		12	89–96		9 July 1911
47	566 [1913]	13	97–104	Pls. 36–41	20 July 1911
		14	105–112		25 July 1911
48	569 [1913]	15	113–120	Pls. 42–47	10 February 1912
		16	121–128		13 February 1912
49	571 [1914]	17	129–136	Notes on figures	15 February 1912
		18	137–144		25 February 1912
50	573 [1914]	19	145–152	Figs. 2–3 Pls. 48–53	11 March 1912
		20	153–160		12 March 1912
51	581 [1919]	21	161–168	Figs. 4–5 Figs. 6–7	15 March 1912
		22	169–176		21 November 1913
52	582 [1920]	23	177–184	Pls. 36–41	25 November 1913
		24	185–192		13 February 1914
53	584 [1920]	25	193–200	Figs. 8–9 Figs. 10–11	21 February 1914
		26	201–208		28 February 1914
51	581 [1919]	27	209–216	Figs. 4–5 Figs. 6–7	29 April 1914
		28	217–224		No date
52	582 [1920]	29	225–232	Figs. 8–9 Figs. 10–11	1 May 1914
		30	233–240		9 May 1914
53	584 [1920]	31	241–248	Pls. 54–59	8 May 1914
		32	249–256		12 May 1914
51	581 [1919]	33	257–264	Figs. 12–13 Pls. 60–63	14 May 1914
		34	265–272		27 May 1914
52	582 [1920]	35	273–280	Pls. 64–68	26 May 1914
		36	281–288		24 May 1914
53	584 [1920]	37	289–296	Figs. 14–15	20 May 1914
		38	297–304		23 May 1914
51	581 [1919]	39	305–312	Pls. 69–73	10 September 1920
		40	313–320		20 September 1920
52	582 [1920]	41	321–328	Figs. 14–15	24 September 1920
		42	329–336		6 October 1920
53	584 [1920]	43	337–344		8 October 1920

(1913: 173–174) subsequently re-described *Contradens*, listing the type species as *Unio contradens* Lea. The date of publication for pages 169–176 is listed as 21 November 1913 (Table 1). The species and subspecies Haas included in *Contradens* are included and discussed on pages 174–202. Pages 169–208 were published between 21 November 1913 and 28 February 1914 (Table 1).

*Uniandra* was introduced as a section of *Ensidens* (Haas, 1912: 140) and *Unio inaequalis* Rochebrune, 1882 was designated as the type species. *Uniandra* was described on page 140 in Haas (1910–1920) which is dated as published 25 February 1912 (Table 1). Unlike

*Contradens*, *Uniandra* was not used in any plate captions in Haas (1910–1920).

The final result is that *Contradens* Haas dates from 1911 and *Uniandra* Haas, 1912. If they are considered congeneric, *Contradens* has priority over *Uniandra*.

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**Arthur E. Bogan**

North Carolina Museum of Natural Sciences  
11 West Jones Street  
Raleigh NC 27601 USA  
Arthur.bogan@naturalsciences.org

## Book Review

Óscar García-Álvarez, Luitfried von Salvini-Plawen, Vietoriano Urgorri, and Jesús S. Troncoso. 2014. **Fauna Ibérica Volume 38 - Mollusca: Solenogastres, Caudofoveata, Monoplacophora**. Museo Nacional de Ciencias Naturales & Consejo Superior de Investigaciones Científicas, Madrid 2014, 295 pp. 978-84-00-09870-4, 27 €. [In Spanish]

This impressive volume compiles vast amounts of data on three of the least understood classes of molluscs, Solenogastres (= Neomeniomorpha), Caudofoveata (= Chaetodermomorpha) (together constituting Aplacophora) and Monoplacophora, and has been compiled by leading experts O. García-Álvarez, L. v. Salvini-Plawen, J. S. Troncoso and V. Urgorri, all of whom have published extensively on the Iberian fauna of these groups. Sadly, Professor Luitfried von Salvini-Plawen passed away on October 20<sup>th</sup>, 2014, while the book was in production, so he never got to see this gem of malacology. Beautifully bound in crimson cloth with the elegant black book cover of the Iberian Fauna series, this book presents a state-of-the-art compilation on these three molluscan classes. Written in Spanish and profusely illustrated, this constitutes the most comprehensive treatment of each of these classes of mollusks, synthesizing anatomical, ecological and systematic aspects of the three groups.

The book begins with a 20-page general introduction to the phylum Mollusca, including historical accounts of the knowledge of the group and utilization by humans, including a brief section introducing the aplacophoran mollusks. These first pages make for very good general reading for those interested in delving into the phylum Mollusca. The book is then divided into its three main sections (with different authors), Solenogastres (pp. 31–163), Caudofoveata (pp. 165–220) and Monoplacophora (pp. 221–252), followed by an Appendix and four colour plates. The three main sections are thorough taxonomic treatments of Solenogastres, Caudofoveata, and Monoplacophora in the Iberian waters down to 3,000 m depth. Each section comprises anatomical and taxonomic treatments including accounts for the natural history, collection, and preservation methods. The book treats 42 Iberian Solenogastres species grouped in 29 genera belonging to 14 families, with taxonomic keys navigating through the taxonomic ranks down to each species. All the taxa are plentifully illustrated, including line drawings of cross sections, sclerites and radula, often accompanied by scanning electron micrographs. Descriptions, geographic distribution, and the biology of each species are provided.

For those unfamiliar with locality names, it would have been very useful to have maps with distribution data. The next section comprises 14 Iberian Caudofoveata in four genera and three families, following the same structure as the previous section, including grayscale photographs of the animals (sadly, these are not of the best quality), and line drawings of sclerites and radular apparatus. Unfortunately, the quality of the illustrations for the Caudofoveata section is not comparable to that of the Solenogastres part, despite both sharing two authors. Finally, the two Iberian Monoplacophora are described, with their key to species; *Laevipilina cachuchensis* is described and illustrated based on scanning electron micrographs of the shell and radula (curiously, the radula is also presented as a line drawing), while *L. rolani* is illustrated by line drawings only (both, the shell and the radula). Appendix 1 provides an extensive nomenclatural list of synonyms and prior name combinations, and is co-authored by M.A. Alonso-Zarazaga, a member of the International Commission on Zoological Nomenclature. The book ends with four color plates with live photographs of 13 Solenogastres, 4 Caudofoveata, and *L. cachuchensis*.

This is a book that many molluscan workers, and all of those interested in aplacophorans, must have. No comparative thorough modern treatment of these groups is available for any region of the world, and perhaps the only one that comes close is Jones and Baxter (1987), but the Iberian Fauna volume includes much more information for each species and many more species. This volume can be purchased in the Spanish Consejo Superior de Investigaciones Científicas publications portal. A good level of Spanish is necessary both for reading the book and for navigating through the website where it can be purchased.

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### Gonzalo Giribet

Department of Organismic and Evolutionary Biology  
Harvard University  
Cambridge, MA 02138 USA  
ggiribet@g.harvard.edu



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THE NAUTILUS publishes articles on all aspects of the biology, paleontology, and systematics of mollusks. Manuscripts describing original, unpublished research and review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of interest to the malacological community will appear in a notices section.

**Manuscripts:** Each original manuscript and accompanying illustrations should be submitted to the editor preferably via e-mail or as hardcopy in triplicate.

Text must conform to the dimensions of 8½ × 11-inch paper, double-spaced, and single-column throughout (including literature cited, tables, and figure captions). Authors should follow the general recommendations of *Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers*, available from the Council of Science Editors at [www.councilscienceeditors.org](http://www.councilscienceeditors.org). The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Metric, not English, units are to be used. Geochronologic modifiers should be capitalized only when units are formally recognized: for instance, use Late Cretaceous but early Miocene. Likewise, only modifiers of formally recognized chronostratigraphic units are capitalized: use Lower Jurassic but upper Oligocene.

The sequence of sections should be title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). If corresponding author is not the senior author, please indicate. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional key words. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabridged. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. If in doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

**Illustrations:** Illustrations are rendered either at full-page width (maximum width 17 cm) or column width (maximum width 8.2 cm). Please take these dimensions into consideration when preparing illustrations. Page-width illustrations ideally should span the entire width of printed page (17 cm). "Tall" page-width illustrations should be avoided, square or "landscape" formats work better. Please design plates accordingly, such that there will be enough space left at the bottom of printed page for plate caption. (Digital technology has made this task much easier.)

All line drawings must be in black, clearly detailed, and completely labeled. Abbreviation definitions must be included in the caption. Line drawings must be high resolution files at least 600 dpi (dots per inch) resolution at actual size. Standard digital formats for line drawings include .tif, .bmp, .psd, .eps, and .pdf.

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If more than one figure is included in an illustration, all figures are to be consecutively numbered (Figures 1, 2, 3, . . . , NOT Figures 1A, 1B, 1C, . . . , NOR Plate 1, Figure 1, . . . ). In illustrations with more than one figure, make sure that blank areas between figures is kept to a minimum, thereby allowing for more area for each individual figure.

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